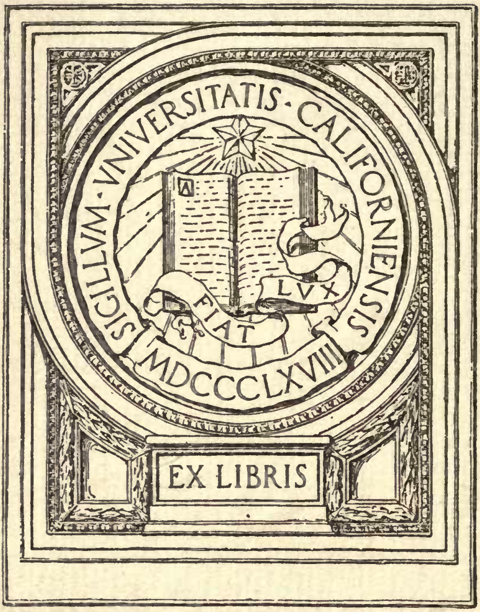
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BOTANY OF THE LIVING PLANT

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Showing proportionately the approximate limit of size of the plant-body. See p. 14, also chapter IX.

(From Figuier's *Vegetable World*.)

BOTANY OF THE LIVING PLANT

BY

F. O. BOWER, Sc.D., F.R.S.

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WITH 447 FIGURES

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PREFACE

THE present volume is framed on the lines of the annual Course of Elementary Lectures on Botany given in Glasgow University for more than thirty years. During that time the Course has been constantly remodelled and developed. The extended limits of a book allow the introduction of additional facts, and the subject-matter has itself been in part expanded. But the main object, that of presenting the Plant as a living, growing, self-nourishing, self-adapting creature, has been maintained throughout the book, as I always endeavour to present it in the Lecture Room.

The Lecture-Scheme has been recast as a series of Essays, each one self-contained. They are designed so as to fit together and form a continuous treatise. The omissions are palpable enough: for no attempt has been made after encyclopedic writing. The material is throughout such as will be reckoned elementary. Elementary and fundamental should be held as equivalent terms when applied to those facts and principles upon which a Science is built. It is to these that the available space has been devoted.

The book has not been written in conformity with the schedule of work prescribed by any University or School, nor is it designed to meet the requirements of any specified examination. Its object has been to present a true picture in as simple terms as possible. Proceeding from the known to the unknown, it opens with a description, structural and physiological, of familiar Flowering Plants. The consequent inversion of the evolutionary aspect of the Vegetable Kingdom as a whole will probably be criticised. It is hoped that the justification of this arrangement will be found in the reasoning and the employment of materials later in the book. Plant-Life presents its problem to any alert mind. It would be a pleasure to the author if not only the student but also the general reader found in these pages the Story of the Living Plant unfolding itself by stages both natural and interesting. If this be so, it should fasten the reader's attention, and so lead him on from the simple facts of the earlier chapters to those generalisations which are discussed towards the close.

More than 200 of the illustrations have been specially prepared for this book. My own original drawings are initialled. An almost equal number have been drawn by Dr. J. M. Thompson, and are signed by him. Many beautiful French blocks have been borrowed from Figuier's *Vegetable World*, and a considerable number are taken, with the permission of the publishers, from Strasburger's *Textbook*. By arrangement with the S.P.C.K., many of the excellent drawings of Fungi by the late Professor Marshall Ward, F.R.S., are embodied. They are taken from his *Diseases of Plants*, a book which has long been out of print. The sources of all these illustrations, and of others not mentioned here by name, are specified in the rubrics, and their use is gratefully acknowledged.

My sincere thanks are offered to two friends who have carefully read the proofs. Professor W. H. Lang, F.R.S., has given the expert criticism of the Botanist; while the other, a member of the lay-public, has made valuable suggestions regarding that clarity of style which is sometimes apt to be forgotten by the technical writer. To both I owe a deep debt of gratitude.

F. O. BOWER.

GLASGOW, *February* 1919.

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BOTANY OF THE LIVING PLANT

INTRODUCTION.

The vegetation of any ordinary country-side consists of a vast number of distinct kinds of Plants, large and small, simple and complex. They are mixed up without any apparent system or order. The scientific study of this mixed vegetation has as its object to get to know as much as possible about the various Plants that compose it. The Form of each kind of Plant when fully grown will have to be noted, as well as the way it grows so as to attain that form. The way the Plants nourish themselves is also an important question. And finally we shall enquire how they increase in numbers: for some die off from time to time, and their places are constantly being taken by new Plants.

This study of Plants and of their vital activities cannot be carried out with success by merely examining the mass of Plants all together. They must be taken singly, and examined individually. One can then be compared with another. On the basis of such comparisons we may form opinions as to their probable relationships, and even approach a view regarding their origin. To make such a study methodical and coherent, the Plants recognised must be arranged according to their characters. They must in fact be classified, and the classification should then indicate their natural affinities. In such a *Natural Classification* those which are relatively simple in their structure and mode of life should be placed first, and the most elaborate last.

We may take as an example of a very simple Plant that green powdery growth which is often found on the bark of Trees, on wooden rails, and other places, in damp situations. This growth is composed of individual grains which are very numerous, but so small that they are only visible to the naked eye when present in large numbers.

Highly magnified, the powder is seen to consist of single spherical cells, or groups of cells (Fig. 1). Each of these cells is an individual Plant, and it multiplies by division. The results of such repeated divisions may remain for a time coherent, thus forming groups of varying number. But finally they separate, and each single cell can continue its life as a distinct *unicellular organism*. It is called *Protococcus*, a name which recognises its simple primitive nature. It would be held as taking a low place in the scale of vegetation, and would be classified near to the beginning of our Series.

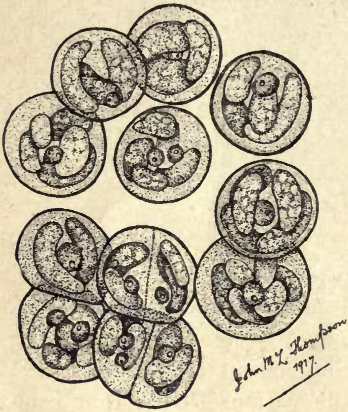


FIG. 1.
Cells of *Protococcus*, some isolated, others, resulting from recent division, are still coherent. (×730.)

On the other hand, ordinary herbs, shrubs and trees are examples of more elaborate organisation. Each one of these is composed of various large and complex parts, which are united to form the complete Plant, and severally serve distinct functions for the benefit of the whole. Such Plants may attain large size, and very complicated structure, as in the case of Forest Trees (Frontispiece). Each of these Plants is an independent individual. Their increase in number is by *Seeds*, produced through the process of Flowering. The production of seed is an involved and elaborate process, as will be seen when it is described in later chapters. Partly on the ground of their complex structure, and partly because of the elaborate method of their propagation, such *Flowering Plants*, or *Seed-Plants*, are ranked as higher in the scale. Between such extremes as *Protococcus* and a Flowering Plant other intermediate types may be ranked according to their structure and their method of increase. And so a Series may be formed leading from those which are comparatively simple, by gradual steps, to those which are more elaborate. Such a Series is believed to illustrate roughly, and with some degree of truth, the course which the Evolution of the Vegetable Kingdom has actually followed. The simpler examples are held to represent such types as appeared earlier in the History of Descent, and thus to be more *primitive*. The types which are more complex in structure, and in their method of propagation, are believed to have appeared later in the History of Descent, and are regarded as *derivative*. This agrees essentially with the sequence of fossils embedded in successive Geological Strata: so that the positive evidence of the Rocks supports, so far as it goes, the grouping of Plants by comparison.

On such grounds as these, Plants may be sorted into five main divisions, each comprising several Classes. They may be tabulated as follows, while examples are given of familiar Plants, illustrating the sort of living organisms which belong to each Class:

Examples.	Class.	Division.
Seaweeds and Freshwater Weeds	Algae	Thallophytes.
Mushrooms, Mildews, Moulds	Fungi	
Mosses	Musci	Bryophytes.
Liverworts	Hepaticae	
Ferns	Filicales	Pteridophytes.
Club-Mosses	Lycopodiales	
Horse-Tails	Equisetales	
Pines, Firs, Yew	Coniferae	Gymnosperms.
Oak, Sunflower, Potato, Bean	Dicotyledons	Angiosperms.
Grasses, Lilies, Palms	Monocotyledons	

The natural way to study these would doubtless be to start from the simplest and most primitive, and to proceed to those which are more advanced:—that is, to follow the course which we believe that Evolution has taken. It is, however, easier to begin the study of the Living Plant from those of larger size, which are already familiar subjects to everyone, than from minute and unfamiliar organisms, which can only be examined microscopically. It will thus be best for us to take the Higher Flowering Plants first, and to hold over the lower organisms to the end.

One further general statement may be made regarding the Series as thus laid out. It relates to the mode of life of the Plants concerned. Many of the Thallophytes are water-growing Plants, such as Seaweeds, and the Algae of freshwater streams and pools, and most of them grow only where abundant moisture is present. The Mosses and Ferns, though they appear as land-living Plants, require external fluid water for completing one essential stage in their life-history: without it they fail. On this ground they may be called the "Amphibians" of the Vegetable Kingdom. But the Seed-Plants are not thus dependent upon external fluid water. The general conclusion follows that Vegetation began in the water, that it spread later to the land, and that it found its climax in the Seed-Bearing Plants of the Present Day. This is the fundamental idea which should underlie all Ecology, that is, the study of Plants in relation to their surroundings. Ecology as practised to-day consists in working out the details of this fundamental thesis. But the broadest of all ecological conclusions is that Plants were in ultimate origin aquatic: that they have gradually emancipated themselves from dependence upon external fluid water: and that the highest terms of the series are characteristically Dwellers on Dry Land.

Conclusions like these have been drawn by Zoologists with regard to the Animal Kingdom. Both branches of living things, viz. Animals and Plants, probably originated in the water. Certain of the very simplest Animals and Plants are so alike that it is difficult to draw any line separating at such early stages the one Kingdom from the other. It is therefore concluded that they probably had a common origin, but that in the course of Evolution they diverged. The most distinctive feature which separates them is that of Nutrition. *Plants advanced along the direct line of Self-Nutrition.* They form their own organic food from inorganic materials. These are ultimately Carbonic Acid and Water, together with Mineral Salts. Their green colouring matter plays an essential part in the process of their nutrition from such simple sources. *Animals*, on the other hand, *advanced along Predatory Lines.* They take their food in more elaborate form as material already organic: that is, either from bodies which are living, or such as have been produced by living organisms. This is seen both in Herbivorous and Carnivorous Animals. Pursuing these divergent lines, both Animals and Plants established themselves upon exposed land-surfaces, and both show in their higher terms abundant evidence of their fitness for living in the surroundings which they have adopted.

Since all Animals take their food as organic material,—that is, in a sense at second hand, and do not construct it for themselves,—it is obvious that at some stage or other they are dependent for it upon the Vegetable Kingdom. This gives Plants a special claim on the attention of Biologists: for *the Green Plant is, in point of fact, the essential source of supply of organised material to all other forms of Life upon the Earth's Surface.*

DIVISION I.

ANGIOSPERMS OR HIGHER FLOWERING PLANTS

CHAPTER I.

SEED. GERMINATION. FORM OF THE ESTABLISHED PLANT.

THE Higher Plants are called Seed-Plants, because they bear Seeds. The *Seed* is a detachable part of the parent Plant, which contains the germ of a new individual. When mature, it is usually hard and dry. It can stand drying up without losing its vitality. In this state it may remain dormant for a considerable period, often for years, and may withstand conditions which would be unfavourable for active life, such as extremes of heat and cold. But when the conditions are favourable, the active life of the germ, which has been in a state of suspense in the dry seed, may be resumed. The test of vitality of the seed is whether or not it will germinate when exposed to suitable conditions.

If a dry seed of a Bean, such as may be bought in a seedsman's shop, be dissected, its parts may be easily recognised. But the dissection will be more readily carried out if it be soaked in water for twenty-four hours. The effect of the soaking will be that it will increase in bulk and in weight. The *swelling* is due to the imbibition of water, which is a general property of organised bodies. A distinction must be drawn between such swelling and growth. Swelling by imbibition is a reversible process, and is not a manifestation of life. A dead bean will swell equally with a living one. If either be dried again, it will shrink back to its original bulk. *Growth*, on the other hand, is a result of vital activity. It involves, as we shall see in Chapter VIII., a redistribution of organic material. This is an irreversible process. The seed which has once germinated cannot be restored to its original state again. It is the same with all other changes in life: *the prior condition can never be exactly resumed after vital changes have occurred.*

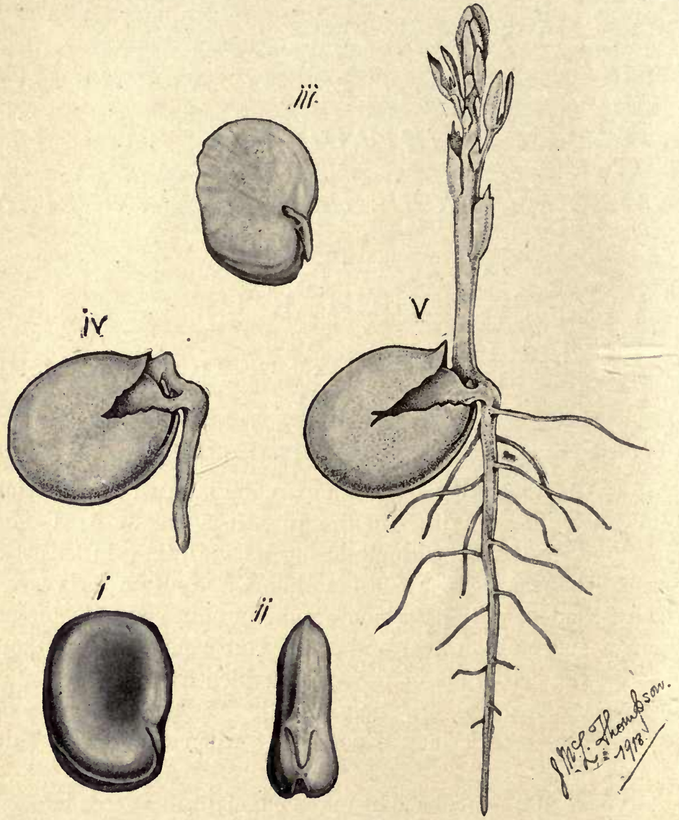


FIG. 2.

Common bean (*Vicia Faba*). i. ii., seed covered by seed-coat. iii., germ, with seed-coat, and the nearer cotyledon removed. iv. v., successive stages of germination slightly reduced.

The Bean-Seed, as shed by splitting of the Bean pod, appears as a roughly discoid body (Fig. 2). It consists of an *embryo* or germ, protected by an external *Seed-Coat.* On its edge, close to a slight involution of the margin, is an elongated scar, the *hilum,* marking the point of attachment to the parent plant. If the tough brown Seed-Coat be dissected off, the *Germ* or *Embryo* will be disclosed, filling the whole space within. It consists of two large flattened *Seed-Leaves*, or *Cotyledons*, which are attached at the base, right and left, to a curved body which lies between them. Part of this is compressed between the Seed-leaves. It is the *leafy bud* or *plumule*, which is to grow into the shoot of the seedling. Pointing in the opposite direction to this is the *first root* or *radicle*, the conical tip of which is close to one end of the hilum. The parts thus recognised are present in all normal seeds of *Dicotyledons*, which take their name from the *paired Seed-Leaves.* But the form and proportions of the seed and of the germ may vary in different plants, and certain additional tissues may in some cases be present. The Seed-Leaves of the Bean are fleshy in texture, and are stored with materials which serve on germination for the nutrition of the other parts of the germ.

The conditions necessary for the germination of a living seed so constructed are: (i) *the presence of moisture*; (ii) *free access to atmospheric air*; and (iii) *a suitable temperature.* The ordinary conditions of spring-time would meet these requirements, if the seed were buried in an open porous soil. For the soil would be moist, and the air would be free to penetrate its pores; while the rising temperature of the season would meet the third requirement in the case of seeds of temperate climates.

Supposing these conditions to have been fulfilled in the case of a living Bean-Seed, *germination* ensues. The first external change is the rupture of the seed-coat at a point close to the end of the scar. Through this the pale young *root* protrudes, and as it elongates its conical tip at once penetrates vertically downwards into the soil. When the root has attained a length of several inches, a curved *shoot* emerges through the slit between the bases of the two seed-leaves. Clearly this is the result of growth from the leafy bud seen between the cotyledons in the seed. This shoot turns upwards, and soon projects above the level of the soil. *Growth* is thus seen in both parts, the material required for the enlarging tissues being supplied from the fleshy seed-leaves. This is used in building up the enlarged root and shoot. No drying-up will make the root or shoot shrink back to their original size or form, nor can the material drawn from the seed-leaves be by any means replaced. *Such growth is an irreversible process, as is all growth in Plants.*

That the root points downwards and the shoot upwards is not a haphazard result. Experiments with seeds placed in various positions in the soil show that the behaviour of these two parts of the seedling is constant, and suggest that it is a response to some external influence that applies to them all. In this case the influence is Gravity. The subject of external influences will be discussed in detail later (see Chapter VIII.). Meanwhile it must suffice to say that an influence such as Gravity, which acts on a living organism so as to produce a change in it, is called a *stimulus*. The response which the living organism shows is called the *reaction*. The effect of Gravity upon the growing shoot or root, so as to make the one turn upwards and the other downwards, is an example of *reaction to stimulus, and such a reaction is one of the essential indications of Life.*

It is familiar to every gardener that, up to a certain point, the higher the temperature the quicker his seedlings appear above ground. But plants vary in their relation to temperature, and that necessary for germination is not the same for them all. Thus most cereals can germinate at a temperature very near to the freezing point, whereas Maize and the Kidney Bean require a temperature of about 9° C. All the functional activities of the Living Plant have such a relation to temperature. The case of germination is merely one example of a general condition of Life. This subject will also be taken up again in Chapter VIII.

The root and shoot established on germination are capable of continued growth, which is followed in both cases by the formation of lateral appendages. Thus a *Root-System* and a *Shoot-System* are established, the former being buried in the soil, the latter rising above the level of the soil, and constituting the part of the plant ordinarily seen (Fig. 2, v.). If the soil be carefully washed away from the root-system of a Bean-seedling after the main root has attained about eight inches in length, it will be seen to consist of a *primary*, or *tap-root*, which grows directly downwards and bears horizontal *lateral roots*. The smallest and youngest of these are nearest to the tip of the main root, and the largest and oldest are most remote from it. These may in like manner bear *lateral roots of still higher order*, radiating in all directions. Thus a complex root-system is built up. The extreme tip of each root comes naked out of the soil, and is pellucid and slimy to the touch, so that it readily slides past obstacles as it penetrates the soil. But about three-quarters of an inch back from the tip the particles of soil adhere to the root, showing that from that point backwards a close relation is established between the root and the soil. It will be seen later that this is due to the presence of *numerous minute root-hairs*.

When the shoot of the Bean has grown to the length of about six inches, it will be seen to consist of a central *Stem* terminated by a *bud*. *Leaves*, of which the lowest are pale-coloured scales, are borne laterally on the stem. Passing upwards from the base successively larger leaves are met, each with broad green lobes and a sheathing base. Passing on from these mature leaves, we come to the bud. Dissection of the bud shows that it is composed of a series of successively more minute leaves, very delicate in texture, closely overlapping one another, and all seated on the shortened axis. *A bud is thus a compact young shoot, consisting of a short stem overlapped by crowded, immature leaves.*

As the shoot develops, a new bud appears in the axil, or angle of insertion of each leaf upon the stem. Even the cotyledons of the Bean may bear such *axillary buds*. They are constructed like the apical bud, and on development each may repeat the characters of the main shoot. Provision is thus made for multiplication of shoots so as to form a *branched shoot-system*.

The Bean-Seed itself has throughout germination remained below ground. Its fleshy seed-leaves do not emerge from the seed-coat, but are there gradually emptied of their nutritive store, and finally rot away. Their sole function is storage of food-material for the germ. But in other plants the behaviour is different. A good example is seen in the Charlock. Its seed is nearly spherical, with slightly flattened sides. A lateral scar of attachment (hilum) is seen, as in the Bean, and the seed is covered by a tough leathery seed-coat. Within this is the embryo, with two cotyledons, a bud or plumule, and a first root or radicle. But here the cotyledons are folded sharply in a median plane, giving a compactness to the embryo, which fills the spherical seed (Fig. 3, i. ii.). On germination the seed-coat is burst by the enlarging germ, and the root emerges as before, curving at once downwards (iii.). But here the part of the stem or axis below the seed-leaves grows quickly in length. At first it shows a strong arching curve (iv.). But later this is straightened out, with the consequence that the cotyledons and the bud are carried above ground, still covered by the protecting coat. It soon falls away, and the cotyledons expand, diverging as green leaves, with the bud between them (vi. vii.). The latter elongates as it grows older, forming the leafy shoot. Thus the parts of the seedling of the Charlock are numerically and relatively as in the Bean, and in both cases the food-supply is in the fleshy cotyledons. The difference lies in the fact that in the Bean the active growth is in the region of the axis *above* the insertion of the seed-leaves; in the Charlock it is in the region *below* them. They are thus raised above the soil, and exposed to the light. They expand as green leaves, and help the nutrition. Thus in the Charlock the seed-leaves serve first for storage, and afterwards for carrying out nutrition. It is not an uncommon

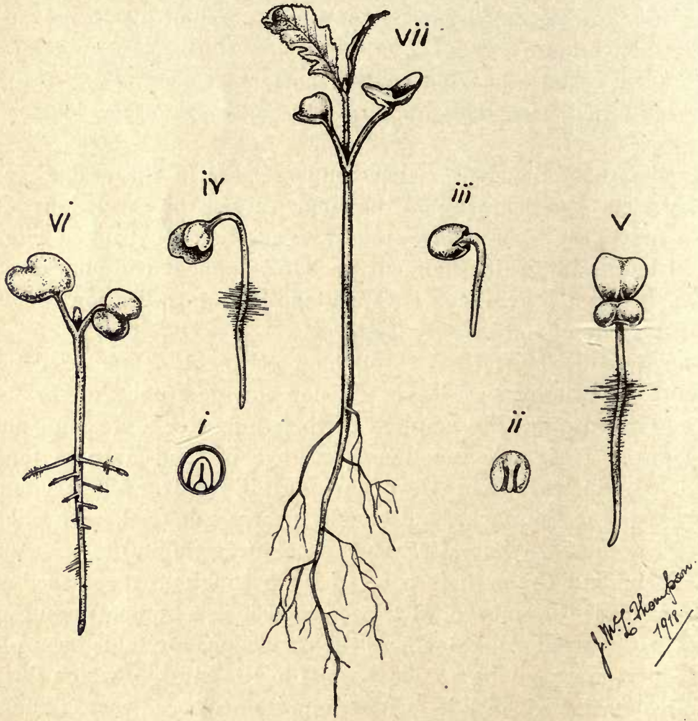


FIG. 3.
Charlock (*Brassica Sinapis*). i. ii., seed with and without seed-coat. iii.-vii., successive stages of germination. Natural size.

thing in plants for a part to serve more than one purpose, sometimes simultaneously, sometimes successively.

A third type of germination may be seen in the Castor-Oil plant (Fig. 4). The seeds are large, and covered by a mottled, brittle seed-coat, which is easily removed, disclosing the semi-transparent contents. These consist of a thin film covering the massive oily *endosperm*, a nutritive store which is not represented in the previous examples. It can easily be split down the middle in the plane in which the seed is flattened (ii. vi.). The germ is then disclosed, having the same number and relation of parts as in the other examples. But here the cotyledons are thin and papery, and the whole germ is immersed in the nutritive endosperm. The chief store of food is thus not in the germ itself, but in the surrounding endosperm.

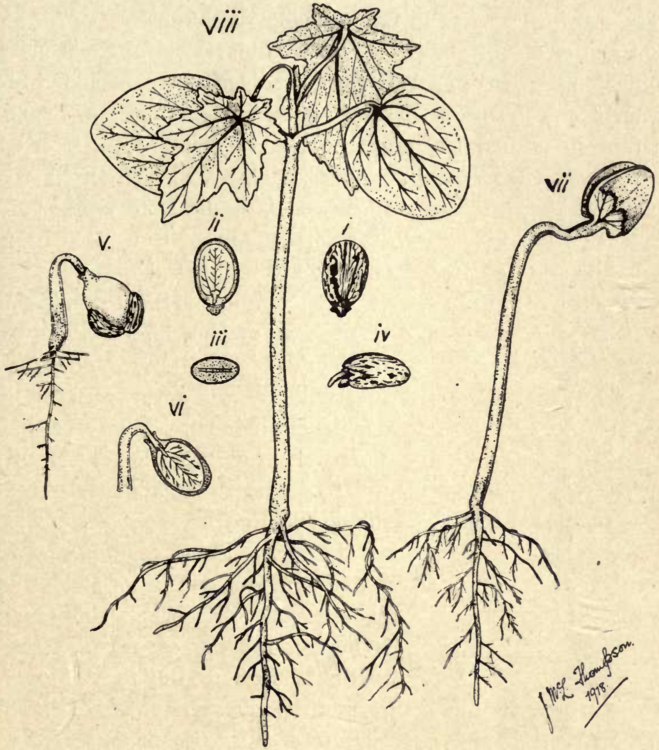


FIG. 4.

Castor oil (*Ricinus communis*). i. ii. iii., seed from outside, in longitudinal and in transverse section. iv. v., seedling with seed-coat burst but cotyledons still enveloped in endosperm. vi, the same cut longitudinally. vii., hypocotyl straightening, endosperm still adhering to cotyledons. viii., established seedling, with expanded cotyledons and first plumular leaves. (½ natural size.)

The germination of the Castor-Oil seed corresponds in its external features to that of the Charlock. But here the germ, lying in close contact with the endosperm, extracts the food from it, and absorbs it into itself, while the endosperm gradually shrivels. As the seed-coat is thrown off, the cotyledons turn green and expand. The dry remains of the endosperm may then be seen still for a time adhering to their lower surfaces; but ultimately it falls away. Here the cotyledons act first as suctorial organs, and later expand into nourishing green leaves. The root and shoot thus established may develop further into a root-system and a shoot-system, as in previous cases.

The leafy shoot of the Sunflower is produced in a manner very like that of the Castor Oil. But it differs from it and also from its own smooth lower parts in having a harsh roughened surface. This is due to *hairs* of various size. The coarser types of them are seated on conical outgrowths, called *emergences*, often of considerable size. Such surface-growths, or dermal appendages as they are called, are inconstant in occurrence, and irregular in distribution in plants, as compared with the foliar appendages. They vary greatly in character in different plants, and being so inconstant, they are held as less important than the axis and leaf.

FIG. 5.
Diagram suggesting plan of unlimited growth of a Flowering Plant, with multiplication of roots and branches.

Such examples as those now given illustrate some of the differences of proportion, and of function which may occur in seedlings, while the general plan of construction is the same. In each case the result of germination is the establishment of a seedling with its root-system in the soil, and its shoot-system exposed to the air. These regions are directly continuous one with another at the level of the soil. Together they form the living and growing organism. They serve distinct functions, but they co-operate in promoting the general life of the plant.

Each of these two regions of the plant-body once established is capable of indefinite extension (Fig. 5). The radicle continues its apical growth, and can form an unlimited number of lateral roots; these may again repeat the process. In all of them also the root-tip may continue to grow indefinitely. Thus a constantly increasing provision is made for the growing plant as regards mechanical support, and physiologically for the supply of water and salts from the soil. On the other hand, the stem is also gifted with continued apical growth, and it has the power of forming an unlimited succession of leaves, of which the oldest are nearest to the base and the youngest distal, while those at the extreme tip are closely grouped so as to form a terminal bud. Further, in the axil, or angle between the base of each leaf and the stem, a fresh bud may appear, which repeats the chief characters of the terminal bud. Each bud is capable of developing into a lateral branch similar to the main shoot, and so on. The increase in number of shoots or of roots is in fact on a very prolific scale. In herbs, such as the Sunflower, Bean and Castor Oil, this mode of development is not carried far; but still the unlimited possibility exists in the plan of their construction.

It is precisely the same scheme carried out further which gives rise to shrubs and trees. In some of them the development upon this plan may be continued for centuries, and the organism may attain very great size and a high complexity of branching. The result of such continued growth may be very well studied on the twigs and branches of trees in winter, when the leaves have fallen, or in the spring when the winter buds are bursting. For instance, on the Horse Chestnut (Fig. 6), each shoot is terminated by a bud, composed of external bud-scales, which enclose the closely folded foliage leaves awaiting expansion in the succeeding season. The woody stem below is marked by opposite pairs of semicircular scars, where the leaves of the preceding season fell away in autumn. Immediately above each scar an axillary bud may be seen, which is capable of developing into a new branch; but frequently these remain dormant as a reserve of branches to be developed only if required. Some distance down the stem a zone will be found marked transversely by many narrow scars close together. This marks the lower limit of the preceding year's growth, and the scars are those left when the bud-scales fell away. Similar

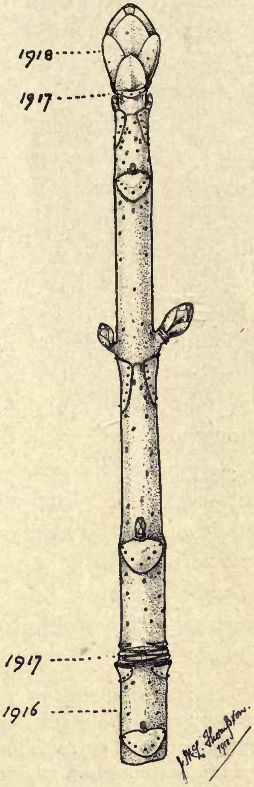


FIG. 6.
Twig of Horse Chestnut in winter, indicating the end of the increment of growth of 1916, the limits of increment of 1917, and the bud to be expanded in 1918, with scars of bud-scales and of foliage leaves, and axillary buds and lenticels. Natural size.

zones may be found successively lower down, marking the limits of the increment of growth of earlier years. Each year's growth leaves its record on the outer surface of the branch. Thus, passing from below upwards along the twig, its annual history can be read, till we arrive finally at the terminal bud, which is already providing for the development of the next year's shoot.

The most important factor in determining the conformation of the plant-body in all the Higher Plants is the continued growth at the apex of stem and root. The life of the Higher Plants may be described as *an indefinitely continued embryology*, while the provision for increase in number of parts is in a geometrical ratio. In this it differs essentially from that of the Higher Animals, in which the parts of the body are laid down once for all in the initial steps of development, and the body is of a circumscribed and limited type.

But though the body of the Plant is thus theoretically unlimited in its plan, in actual practice limits are imposed. It would be a physical impossibility to develop all the potential parts of so complex a system. Many buds remain dormant. In others seasonal conditions may check or stop apical growth. Various mechanical or physiological injuries may intervene, caused it may be by wind or frost. Animal or fungal attack may destroy many embryonic buds. But probably the most potent check of all is the physiological drain of flowering. This is particularly effective in the case of herbs, and especially of annuals, as in the Sunflower or Bean. By such influences the theoretically unlimited plan of development is restricted within bounds.

When speaking thus of a theoretically unlimited plan of development it is necessary to make a reservation. The plan itself is one which has no limit; but in practice an extreme limit is imposed by the principle of similar structures. In similar structures varying in size the strength increases as the square of the dimensions, while the weight increases in the higher ratio of the cube. For every structure, whether living or not, there will accordingly be a limit of size beyond which that structure cannot be enlarged, and still maintain its form, unless there be either a change of plan, or a difference of material. This principle recognised by Galileo has been applied to animals and plants, and explains many peculiarities of large organisms. The greatest height has been calculated to which a tree of given proportions and materials can grow, and still hold itself erect. Some of the tallest trees have approached that limit, which is somewhere beyond 300 feet. Examples of this are seen in the giant trees of California (Frontispiece). The expressions used in the preceding paragraphs naturally apply to organisms of moderate dimensions, and especially to the plan of their construction.

It is upon a scheme such as that laid down in the preceding pages that the body of all the Higher Plants is constructed. The number and exact position of the leaves may vary, and consequently the number and position of the branches, since these arise from axillary buds. The form and proportion also of the axes and leaves is open to great difference of detail, according as they are adapted biologically to the conditions under which they live. But these are only minor modifications, which may make the plan more obvious in some cases than in others. Examination of ordinary herbs, shrubs and trees from the point of view suggested here should be practised upon the varied vegetation seen on any country walk. Such observations will show the constancy of the scheme of organisation of the Higher Plants, even in complicated cases. They will also illustrate in what various ways the number, form and proportion of the parts may differ. Thus there comes about that great diversity in appearance shown by the plants that make up ordinary vegetation, though underlying the construction of them all there is still a consistent plan. *The salient feature of this plan of construction of the Higher Plants is the capacity for an indefinite vegetative increase in size and complexity of the individual, which is based upon their "Continued Embryology."*

CHAPTER II.

THE CELLULAR CONSTRUCTION OF THE PLANT.

THE apical points of Stem and Root, described in the previous chapter, cannot fail to have attracted attention, by reason of their continued powers of growth and of forming new parts. The perpetual youth of the extreme tips is their leading character. Passing back from these we see parts in successive stages of development up to full maturity. This shows from *external observation* that new parts originate there. To understand how this takes place, a study of the *internal structure* will also be necessary. Such study is called *Anatomy*, for in large and solid bodies such as these it is by cutting into them that their construction can best be made out. Two courses are open for such study. A start may be made from the *mature* parts, such as the fully formed stem, leaf, or root, in which the structure is very complicated. Or the young *embryonic* tip itself may be examined first. Since the construction is much simpler at the tip where the tissues are still young, it will be found best to take this first. Moreover, upon the result of this examination it is possible to base a general idea of the construction of the whole Plant-Body and of all its mature parts.

If an apical bud of a water-plant, such as *Hippuris* or *Elodea*, be dissected under a magnifying power of ten to fifteen diameters, a succession of overlapping leaves will be found, those lying within being constantly smaller than those outside them. The series may be followed till the last are too minute for recognition with the simple lens. In the centre is a projecting cone of soft colourless tissue, with a dome-like ending. This is the *apex of the stem, or growing point* (Fig. 7).

If a median longitudinal section be cut through a bud of *Hippuris* so as to traverse this cone to its extreme tip, it would on microscopic examination show that it is not of uniform texture, like paraffin wax. It is built up of a number of structural units, or *cells*, of more or less

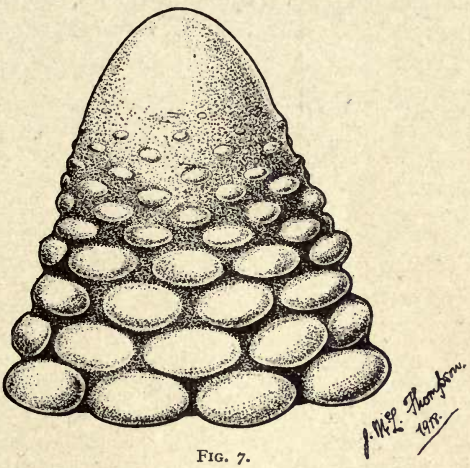


FIG. 7.

External view of the growing point of *Hippuris*, showing the smooth apical cone bearing alternating whorls of lateral leaves, the youngest nearest to the tip. Magnified.

cubical form, which are all essentially similar, and are arranged with some degree of regularity (Fig. 8). More highly magnified, they are seen to be all separated from one another by definite, but very thin *cell-walls*

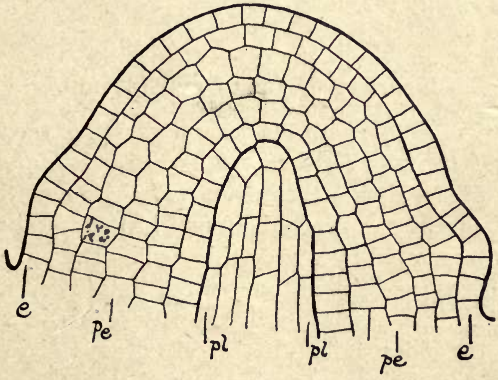


FIG. 8.

Median longitudinal section of the apex of a quite young bud of *Hippuris*. *e*=epidermis. *pe*=periblem. *pl*=plerome. After De Bary. (×300.)

(Fig. 9). Each unit comprises a granular mass of material, colourless and semifluid in the living state, which is the *cytoplasm*. In a central position in each of them is a more highly refractive, spherical body: this is the *nucleus*. Embedded in the cytoplasm, and often difficult to observe, are other minute roundish bodies, which are colourless: they are the *plastids*. The collective term *protoplasmic body*, or

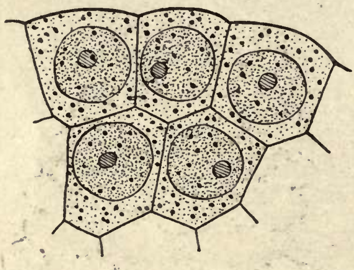


FIG. 9

Young thin-walled cells from the growing point of *Tradescantia*, each with a relatively large nucleus, containing a highly refractive nucleolus. Many plastids are present in the cytoplasm. After Schimper. (× 800.)

protoplast, is applied to all the contents enclosed within the cell-wall. In older tissues the cell-walls are often so conspicuous that the units of construction were called "*cells*" by the earlier observers, from their comparison with the partitioned honeycomb. That name is still retained for them. But it is now fully recognised that *it is the protoplast and not the cell-wall that is the essential part, for it is in it that the active vitality is centred.*

Increase of Cells by Division.

As the tissues increase with the general growth of the apical region, *the number of the cells composing it increases by cell-division.* An examination of the tissues themselves will show how this is carried out. Very frequently cells may be found in the apical cone grouped in pairs, and separated by a very thin wall. These plainly indicate a division of a pre-existent mother-cell into two, usually equal daughter-cells. The new cell-wall thus formed is inserted at right angles upon the older walls. If the cells always divide into nearly equal halves, and if the new walls are fixed at right angles upon the older walls, the result must necessarily show some degree of regularity in the arrangement of the cells that are formed. In some cases that regularity is very striking. The scheme of construction in the case of the apex of *Hippuris* would be like that shown in Fig. 10, and it is found that in plants at large the young tissues are arranged according to similar schemes. Thus in the young state the axis, and, it may be said more generally, the plant-body throughout, is partitioned up into cells in somewhat the same way as a house is partitioned into rooms. And their arrangement is not at haphazard, but according to rule. *It may be stated generally, as a fact of experience, that the whole of the plant-body, whether young or mature, is made up of such cells, or their derivatives.* This generalisation used to be spoken of

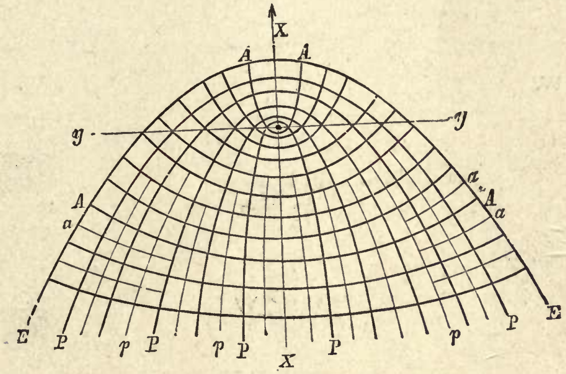


FIG. 10.

Diagram illustrating the plan of arrangement of cell-walls in the apex of the stem of an Angiosperm. XX = axis of construction. EE = external surface. PP = periclinal curves. AA = anticlinal curves. (After Sachs.)

as the "cellular theory." But it is now so fully demonstrated that the fact may be enunciated as a positive conclusion. It will be seen later what are the modifications which such cells undergo so as to produce the mature tissues of the plant, which often differ widely in form and structure from the young cells that give rise to them.

From a comparison of cells in various states of division it is possible to construct a connected history of the process (Fig. 11). The nucleus takes the initiative (i.-iv.). By complex changes, which will be described in detail later, it divides into two exactly equivalent parts, which at first lie in the longer axis of the cell, embedded in the still undivided cytoplasm (v.-vii.). Then a delicate film of cell-wall is formed between them, inserted at right angles to the pre-existent walls, cutting the cell into two nearly equal parts, each containing a nucleus (viii.-ix.). Such simple divisions are called *somatic*, belonging to the *soma* or *plant-body*, to distinguish them from certain divisions which involve further complications connected with the reproductive process. The number of somatic divisions is indefinite, and the numerous cells to which they give rise are while young thin-walled, and all alike.

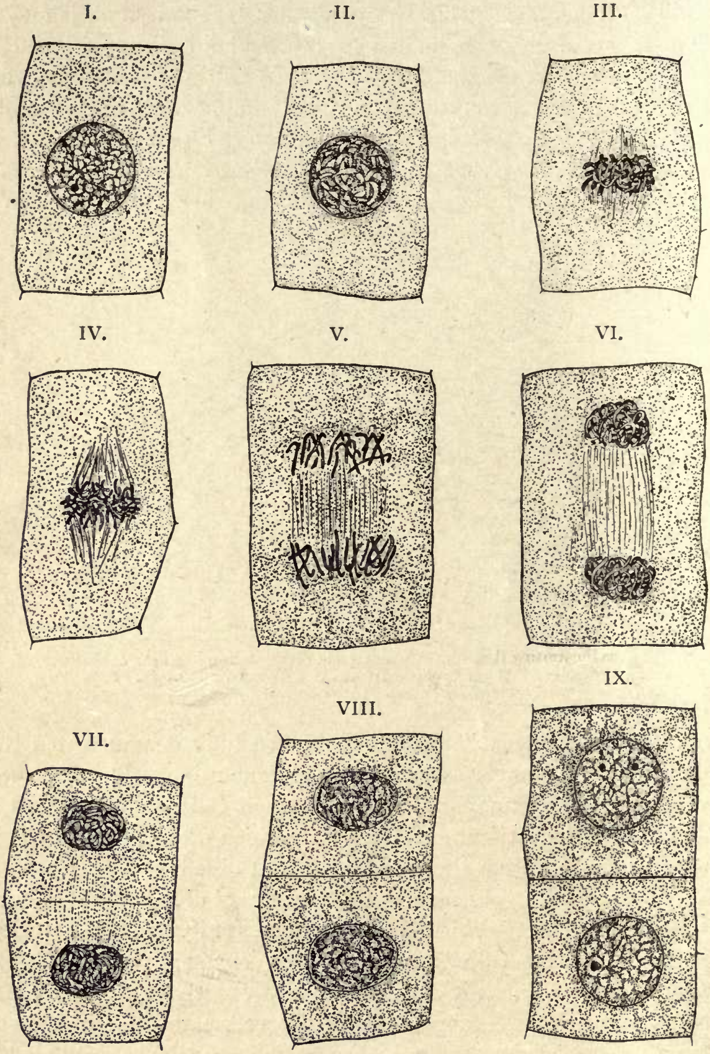


Fig. 11.

I.-IX. Successive stages, drawn from different individual cells of the same root of *Allium cepa* by Dr. J. M. Thompson (× 730). They illustrate the steps in the process of division of a vegetative cell. Such division accounts for the normal increase in number of cells in the "soma," or plant-body: it is therefore called somatic division. Details of behaviour of the nucleus in division will be given later (Chapter xxxi.).

The division of the cell being constantly as described, it follows that every cell arises from a pre-existent cell, and every nucleus is derived from a pre-existent nucleus, by division. The plastids also multiply by division. *None of these constituent parts of the cell are known to be ever produced* de novo, *but are always, like the plant itself, the descendants of progenitors of like nature.* It is different with the cell-wall. In cell-division it appears as a new film deposited from the protoplasm, while, as we shall see, it may be absent altogether from reproductive cells. It is thus a body of secondary importance, as compared with the more constant constituents of the cell.

Differentiation of Tissues.

Passing in the examination of the longitudinal section of any bud from the growing point downwards, successively older tissues

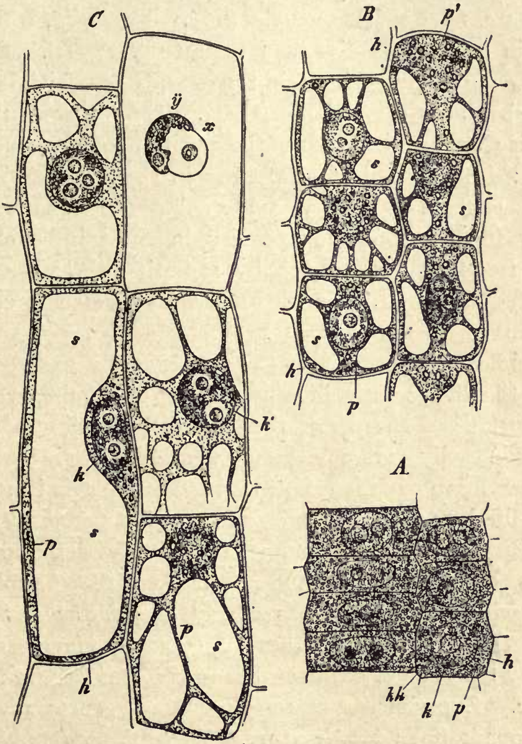


Fig. 12.

Parenchyma-cells from the cortex of the root of *Fritillaria*: longitudinal section (× 550). *A*, very young cells, not yet vacuolated. *B*, older cells with numerous vacuoles containing cell sap, *s*, each surrounded by the protoplasm, *p*. *C*, older cells, with larger vacuoles filled with sap, *s*. The protoplasm (*p*) lines the cell-walls internally, and embeds the nuclei (*k*), which may be suspended centrally, or placed laterally. The large cell to the left has a single large central vacuole, or cell-cavity. (After Sachs.)

are seen, till the mature parts are reached. Various changes appear in the cells. They alter their form and the character of their walls and contents. This leads to *differentiation* of the several types of tissue which compose the mature parts of the shoot. As a rule the cells enlarge greatly. An important change in the cytoplasm, which is usual in plant-cells, accompanies this growth. It is known as *vacuolisation*, and it may be well illustrated in the cells developing into the pith or cortex of an ordinary stem. Starting from the embryonic state, where the wall is very thin, and the cytoplasm and nucleus fill the whole space enclosed by it (Fig. 12, *A*), the volume begins to increase with age and the wall thickens. But the volume of the cytoplasm does not keep pace with that of the whole cell, and vesicles or drops of clear fluid appear within it. These are called *vacuoles*, and they are filled with vacuole fluid, or *cell-sap*, which is water with certain substances dissolved in it (Fig. 12, *B*). The vacuoles are always completely enclosed in the cytoplasm, which controls them and the substances dissolved in them. The vacuoles may vary in number, size and position, and the position of the nucleus is also inconstant; sometimes it lies laterally in the peripheral cytoplasm; usually it is central. As the vacuoles enlarge they may run together, and finally form a continuous cavity in the middle of which the nucleus is frequently suspended by radiating threads of cytoplasm (Fig. 12, *C*). A condition is thus arrived at which is characteristic of many cells in the mature state.

The vacuolated condition of the cell may be more conveniently studied in the living state in cells forming the hairs, which project from the surface of the plant, than in those forming a solid tissue. Such hairs can easily be removed and mounted living in water (Fig. 13). Careful observation will then show that the cytoplasm is not quiescent, but during life it carries out more or less active *movements*. Granules embedded in the cytoplasm may be seen gliding back and forth along the threads that suspend the nucleus, or along that peripheral film of cytoplasm which in living cells always completely lines the wall internally. The rapidity of these circulating movements may be measured by the time a granule takes to traverse one unit of a micrometer scale. Experiments at varying temperatures show that the rapidity depends upon temperature. There is an *optimum* temperature at which the movement is most rapid, and *maximum* and *minimum* temperatures at which it ceases. Anaesthetics and the absence of oxygen stop it. Exposure to the temperature of boiling water, or to poisons such as alcohol, also stops the movement, for these

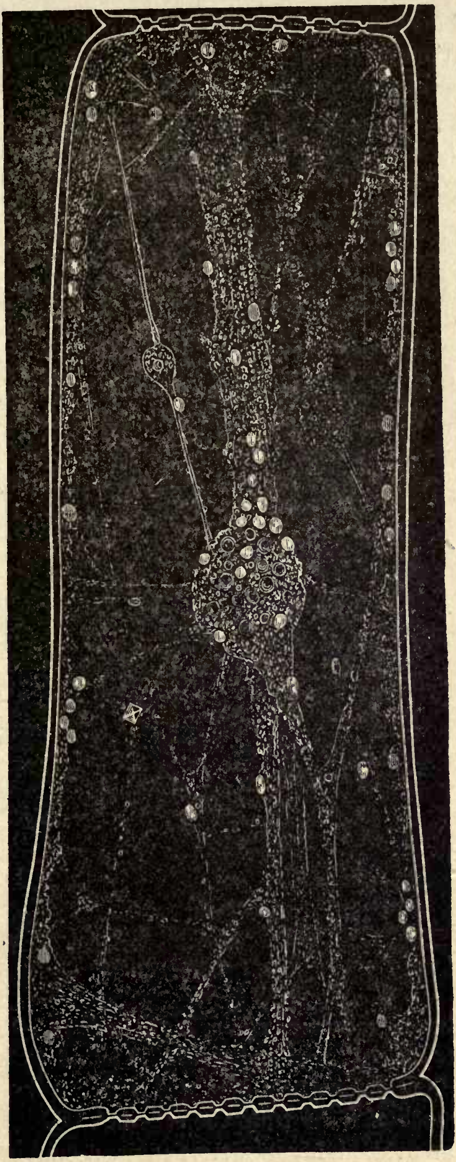


FIG. 13.

Optical longitudinal section of a single cell from the middle of a hair of the Cucumber. Externally is the cell-wall. Its inner surface is lined by a layer of cytoplasm surrounding a large vacuole. In this the nucleus is suspended centrally by numerous cytoplasmic threads. Movements may be seen in these during vitality which convey granules, plastids and even crystals, thus showing active circulation within the living cell. (After Sachs.)

conditions kill the cell. These movements are then *indications of life*, and their relations to temperature and other external conditions are similar to those of other vital phenomena.

Observations on the rapidity of the movements in the parenchyma of the stem of *Elodea* in relation to temperature show that at 0° C. there is no movement. With a rise of temperature the movement begins about 1° C. and increases in speed up to 36° C., which is the *optimum*. On further raising the temperature the *maximum* is reached at 40° C., where movement stops. The *optimum* and *maximum* temperatures in such cases appear to be always near together.

Turgor of the Cell.

Such cells as these give evidence also of another important feature common in the living cells of plants, viz. *turgescence*. If the length of a cell of a living tissue be carefully measured in the normal condition, and the cell be treated with a 5-10 per cent. solution of nitre, or

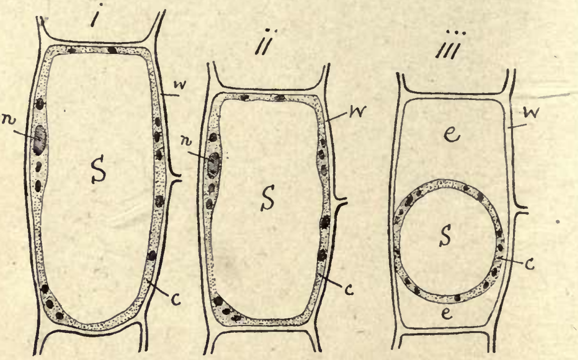


Fig. 14.

Young parenchymatous cell (i.) in the turgid state, (ii.) after treatment with 4 per cent. solution of nitre, (iii.) in 10 per cent. solution of nitre. *w*=wall; *c*=cytoplasm; *n*=nucleus; *s*=cell-sap; *e*=nitre-solution which has passed through the cell-wall. (After De Vries.)

of common salt, and measured again, it will be found that its length has decreased. Its other dimensions would be found to have diminished also (Fig. 14, i.-ii.). Presently it would also be seen that the cytoplasm had contracted away from the cell-wall. Frequently it rounds itself off into an oval, highly refractive mass, occupying the middle of the cell. This is the state styled *plasmolysis* (Fig. 14). If the effect of the agent be watched, it will be seen that the shrinking of the cell happens first, then that the cytoplasm separates from the angles of the cells, and its contraction proceeds until, as it appears, a balance is struck between internal and external influences, and the condition becomes quiescent. The explanation of these facts is found in changes of the *internal turgor* of the cell. In normal life, the protoplast exercises a stretching influence upon the cell-wall, keeping it tight and tense like the outer cover of a pneumatic tyre.

The *state of turgor* thus seen in the living cells of plants originates from the fact that the cell-sap is a solution of salts and sugars, etc., and that the living cytoplasm, which completely surrounds it, behaves as a *semipermeable membrane*: that is, it exercises control over the passage of those substances outwards, though it allows the passage of water inwards. The cell-wall is, however, a permeable membrane, allowing passage to both. As the solutes in the cell-sap tend to absorb water so long as this is available (as indeed it is normally in the living plant), water will then pass into the cell-cavity, increasing the volume of the cell-sap, and of the cytoplasm round it, and the cell-wall will be stretched. This goes on till the power of absorption is balanced by the resistance of the distended cell-wall. Measured in terms of atmospheric pressure the turgor of a living cell is commonly the equivalent of 5 atmospheres, and may in some cases be as high as 25. What happens when a living cell is plasmolysed is that instead of pure water bathing the outside of the cell, a salt-solution is presented, which exercises a counter-osmotic influence to that of the solutes in the cell-sap; and if thc outer influence be stronger than the inner, then water will flow out through the cytoplasm and plasmolysis results. But the film of cytoplasm, being the controlling limit between the two solutions, it will contract away from the cell-wall, which is readily permeable. This continues till a balance is struck between the external solution and the now concentrated cell-sap. Meanwhile the stretching influence of the cytoplasm on the cell-wall is relaxed when plasmolysis occurs, and the cell as a whole shrinks.

The turgor of the cell depends upon the ability of the cytoplasm to control the passage of soluble substance inwards or outwards, and to select those which shall be absorbed or retained. It may be ranked as a vital phenomenon. If the cell be killed, by high temperature or by poison, that power is lost. This may be beautifully shown in preparations of cells in which the cell-sap is coloured, if they are mounted alive in water. The tissues of the Red Beet, or the superficial cells of the Rhubarb leaf will serve. So long as the cells are alive they retain control over the dissolved colouring matter, even after plasmolysis. When they die that control is lost, and the colouring matter diffuses out freely into the surrounding water. *Such control is thus shown to be a property of the living cytoplasm.*

The control over soluble substances by the living cell is physiologically most important. But not less is the *mechanical importance* *of turgor*; for upon it depends that crispness of succulent parts, which they lose on wilting or withering. The relation of the turgescent cytoplasm and the resistant cell-wall is like that of the bladder and skin of a football, or of the inner and outer tubes of a pneumatic tyre. When these are inflated they are firm and rigid; when deflated they are flaccid and limp. So it is with the plant-cells. But here it is fluid, not gaseous pressure. The effect of a fall in pressure is seen in any wilting plant. Withering is the result of the water-supply being insufficient to secure the turgor of the cells. If sufficient water

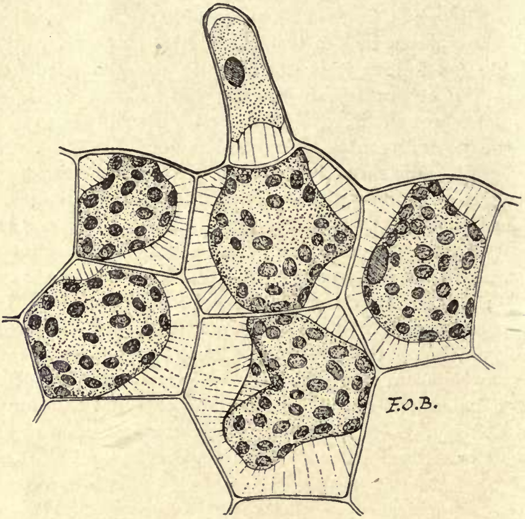


FIG. 15.

Cells from the prothallus of *Nephrodium villosum* after treatment with 3 per cent. solution of common salt (× 550). Drawn as observed about 15 minutes after plasmolysis; the threads are very fine, but appear proportionally thicker in the figure than they actually are.

be supplied to the still living cells of a wilted plant, their turgor will be resumed, and it will recover its firmness. Similarly, the artificially plasmolysed cell loses its mechanical firmness, like a deflated tyre; but may resume it when the plasmolysing salt is washed away, provided that the cell still maintains its life.

The relation of the cell-wall to the cytoplasm is not a mere juxtaposition of two quite distinct things, like the bladder and skin of a football. That their connection is more intimate is shown by the fact that on plasmolysis being carried out carefully and slowly, fine threads of cytoplasm may be seen to stretch from the wall to the contracted mass (Fig. 15). This indicates an intimate relation, quite in accordance with the fact that the cell-wall takes its origin from the cytoplasm. The material required for the growth of cell-wall is deposited from the cytoplasm, as successive layers of cell-wall substance, on the inner surface of the growing wall. Such facts confirm the conclusion that the cell-wall though important, is not a dominating influence in the cell. *It is in the protoplasm that the vital activities reside.*

Changes in the Cells during Differentiation.

It will be well, as a preliminary to the study of the mature tissues to be described in the next chapter, to explain briefly and to tabulate the chief changes which may be traced in the differentiation of tissues at large from the embryonic cells of the apex.[1]

(1) *Changes in Size and Shape of the Cells.*

Practically all cells grow as they mature, and a simple case has been seen in Fig. 12 (*A-C*). But they may also assume various shapes.

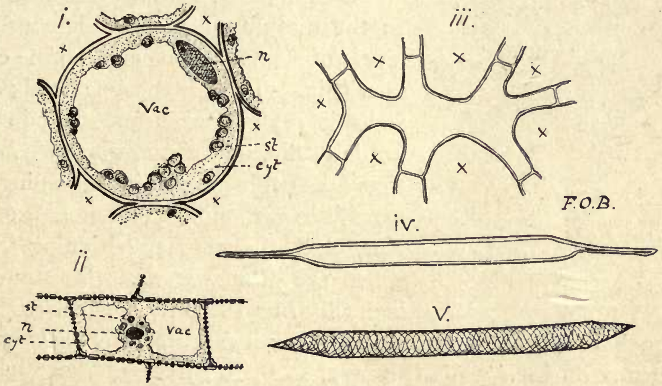


FIG. 16.

Various forms of cells. (i.) cell of the parenchyma from the cortex of the root of a Buttercup, almost spherical; (ii.) oblong cell of the medullary ray of Lime; (iii.) stellate parenchyma of pith of the Rush; (iv.) wood-fibre of the Lime; (v.) fibrous tracheid of Lime.

x=intercellular spaces; *n*=nucleus; *cyt*=cytoplasm; *vac*=vacuole; *st*=starch-grains. (i. ii. iii. × 200; iv. v. × 75.)

In the case quoted the change is slight. Usually there is elongation, and the ends become more or less oblique. Such changes often

[1] This analysis of the changes during differentiation finds its proper place here, and forms the natural foundation for any rational study of mature tissues. But it is open to the student to read it either before or after those tissues have been described, or both before and after.

involve a readjustment of the cells among themselves by a sliding process, which is specially obvious where the cells become elongated or very wide when mature. They seem then to push the surrounding cells aside. Special names used to be applied to all the different characteristic forms of cells. But this is not necessary except in extreme cases; thus the old name *parenchyma* is kept for a tissue of roughly spherical or oblong cells with square ends, while long thick-walled cells with pointed ends are called *fibres* (Fig. 16, i.-v.).

(2) *Changes in the Thickness of the Wall: Pits.*

During the growth of the cell the wall is stretched, and like a rubber sheet it would become thinner as it yields, were it not for the deposit of new cell-wall substance by the cytoplasm. In ordinary cell-walls this is effected by *apposition of successive layers* upon the surface of the wall, and so quickly that the stretching wall, even of an enlarging cell, actually grows thicker. In the mature cells with thick walls the layers of stratification can often be clearly seen (Fig. 17). But the thickening of the walls is seldom uniform. Certain areas are left thin, and a noteworthy feature is that the thin areas in adjoining cells usually correspond. Such areas are called *Pits*, and the thin partitioning wall is called the *pit-membrane*. Pits are of use in facilitating the physiological communication between cells, and practically all mature cells show pits of some sort on their walls (Figs. 17, 18 *B*, 19 *B*).

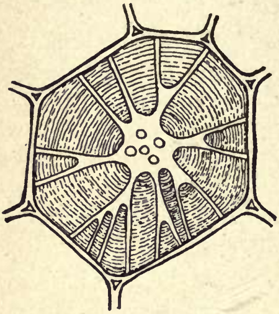


FIG. 17.

Section of a cell of *Hoya carnosa*, with greatly thickened, stratified, and pitted walls. The pits are very narrow, and often branched. (After von Mohl.)

(3) *Changes of Substance of the Cell-walls.*

In the young state the cell-walls are composed of a carbohydrate substance, *cellulose* $(C_6H_{10}O_5)_n$, with more or less of those pectin-substances which form the basis of fruit-jellies. But as they become mature the chemical and physical nature of the walls may change. Some walls become *lignified or woody*, and are then mechanically more resistant and harder. Others become *suberised*, or *corky*, and are then impervious to the passage of fluids. Others may become *gummy*, or *mucilaginous*, and are liable to swell greatly on access of water, which they thus retain. By such changes the cells may be adapted to perform different specific functions.

(4) *Absorption of Cell-wall.*

Though in the young cells the wall completely encloses the protoplasm, it may be partially broken down and absorbed before maturity. This most commonly occurs in those longitudinal rows of cells which

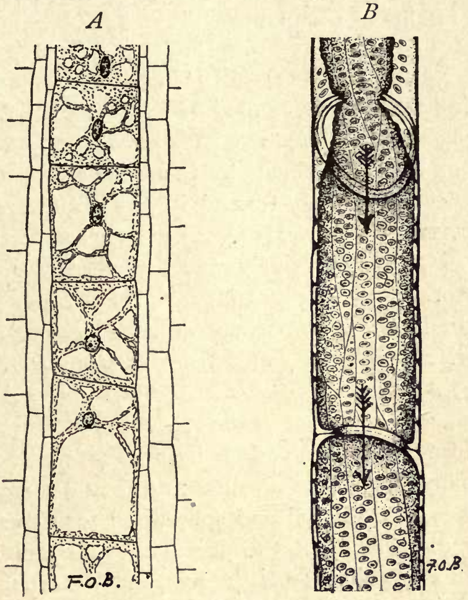


FIG. 18.

A, a longitudinal row of cells from the root of Maize, still with complete septa, nuclei, and cytoplasm, from which a vessel would be formed by absorption of the septa, and disappearance of the protoplasts. *B*, a mature vessel of Sunflower, with thickened and pitted walls and no protoplasmic contents, cut in slightly oblique longitudinal section. The arrows indicate free passage through holes formed by absorption of the septa. The longitudinal lines on the pitted walls show the limits of the adjoining cells. (*A* × 100; *B* × 165.)

are to form *vessels*; and usually it affects the transverse, but sometimes also the longitudinal walls. The septa between the cells being thus removed, two or more cells may be thrown together so as to form a continuous tube. Such a tube is called a *Vessel* (Fig. 18). Other cases of absorption of walls may also occur, but that leading to the formation of wood-vessels is the most important, and the most common.

(5) *Changes in the Protoplasmic Body of the Cell.*

The common change of *vacuolisation* has already been described. Other changes result in the deposit and removal of contained bodies, such as oil-globules, starch-grains, or crystals in the cytoplasm. But the most marked change is in the disappearance of the protoplasmic body itself, so that it is not represented in the mature structure. This is found in the vessels of the wood, and in some other tissues (Fig. 18, *B*). Since the vital activities reside in the protoplasm, those tissues where it is absent, consisting only of cell-wall, are no longer actively living, though passively they may still perform functions important in the life of the plant.

(6) *Changes in the Plastids.*

These bodies are minute, and difficult to see in the young cells (Fig. 9). But as the cells mature they may become more numerous by division, and more prominent by their size and colour. In many cells of vegetative parts they turn vivid green, and are called *chloroplasts*, or *chlorophyll-corpuscles* (Fig. 72). They are present in myriads in any green leaf, and collectively give the green colour to the parts in which they occur. Other plastids may take red, or yellow colours, as in petals, or in fruits, and they are called *chromoplasts.* Others remain colourless, and are called *leucoplasts*, or *starch-forming corpuscles* (Figs. 79, 81).

By such changes as those described the young embryonic cells may be transformed into the various tissues that make up the mature parts. Originally these were all alike; as they become mature they are liable to be differentiated and specialised for different functions. It may be held as probable that what is seen in the individual development is a reasonable guide to what actually took place in the evolution of the race. It is probable that plants with little or no differentiation of tissues, that is Cellular Plants such as the Algae, preceded in the history of Evolution the more complex Vascular Plants, such as the ordinary Land Plants structurally are.

Continuity of Protoplasm.

The cells of living tissues all share in a common physiological life, and are in intimate relation to one another. The cell-walls separating adjoining cells do not form complete barriers between the protoplasts. In most mature tissues a *Continuity of Protoplasm* may be demonstrated, from cell to cell. It is established by means of fine *connecting threads.* These traverse for the most part those thinner areas of pit-membrane, where the distance to be traversed is the shortest. Occasionally they may also extend through the thicker regions of the cell-wall. Examples are shown in Fig. 19, *A*, *B*. The prevalence of Protoplasmic Continuity, now generally demonstrated for the tissues of Plants, forms a structural foundation for their physiological study. There is reason to believe that the protoplasm is the seat of physiological activity, since the protoplasm of the several cells is connected by threads traversing the cell-walls, whole tracts of tissue will be able to share a common life. This leads us to expect that organs will

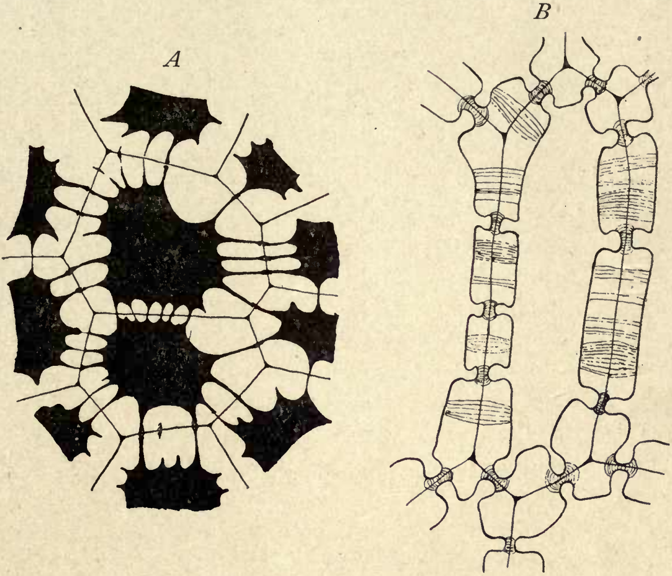


FIG. 19.

Continuity of protoplasm through the walls of plant-cells. *A*. Cells of the pulvinus of *Robinia*, after treatment with sulphuric acid to swell the walls, and staining of the protoplasm with methyl violet. (× 550.)

B. Cell-wall of a single cell of the endosperm of *Lodoicea*, showing the pits and the protoplasmic threads, traversing both the thin pit membranes and the thickened regions of the wall. (× 400.) (After Gardiner.)

react as a whole under external stimulus, and that though the cell may appear to be an individual structural unit, still each cell takes its place as a constituent of that physiological commonwealth which we call the Plant-Organism.

While we thus recognise the physiological importance of the continuity of protoplasm through the cell-walls, it should be remembered what circumstance it is that has made it necessary. It is the presence of the cell-wall itself. The encysted state of the cell is a feature of all advanced types of Plant-Organisation. It was probably secondary in origin, and it is amply justified by the strength and protection which it affords to the defenceless protoplast. Moreover, it has made possible the building up of large mechanically stable plant-bodies, whether buoyed up in water or supporting themselves in air. The presence of cell-wall may appear to have complicated the problem of physiological interchange by interposing barriers between the protoplasts. But this difficulty has been surmounted by those threads of protoplasm, which traverse the walls, and link up the protoplasts into a *continuous living system*.

CHAPTER III.

THE TISSUES OF THE STEM.

THE *mature tissues* of a Plant are not homogeneous as in the apical bud. At first they are all soft. But as they pass over to the mature condition, while certain tissues retain their relatively thin-walls, others become indurated, forming strands which are mechanically resistant. This is illustrated in a familiar way in the shoots of garden vegetables. If these are allowed to mature too far they become stringy, owing to the development of toughened strands. Where the succulent tissues preponderate the harder strands form isolated threads embedded in the softer tissues. In other cases they may be fused into larger tracts, and this is especially so as they grow older. They thus form in tree trunks and twigs of woody plants a cylindrical core, from which smaller strands extend outwards into the leaves and branches. The mature Shoot, with its constituent axis and leaves, is thus composed of a relatively firm skeleton, consisting of the *Fibrous* and *Vascular System*: this is embedded in the softer *Ground-Tissue*; and the whole is covered on the outside by a continuous skin of the *Epidermis*. The first of these serves for *conduction*, and gives *mechanical strength*: the second carries on the functions of *nutrition* and *storage*: while the epidermal system gives *external protection*.

In order to obtain a more exact idea of the general construction of the shoot of a Flowering Plant it is possible either to dissect out the firmer strands by hand, or to study their position by sections. It is only in large and herbaceous plants that the former method is effective; but it is well to carry it out in some such plant as the Sunflower, for this gives a better understanding of the results obtained by sections. By either method it is possible to trace the course and connections of the strands through the softer tissues, and so to construct the vascular skeleton of the shoot. Such a skeleton is shown for

Clematis in Fig. 20. Here the leaves are arranged in pairs, and from each leaf three vascular strands pass into the stem. Each strand curves downwards before reaching the centre of the stem, and after taking a straight downward course to the level of the next pair of leaves it forks. The two shanks are then inserted right and left upon the strands that enter there. If a transverse section be cut at any point between the pairs of leaves, the section shows six main strands arranged in a ring, with smaller strands between them (Fig. 21). A very simple connected system of vascular strands is thus formed, and it illustrates the arrangement usual

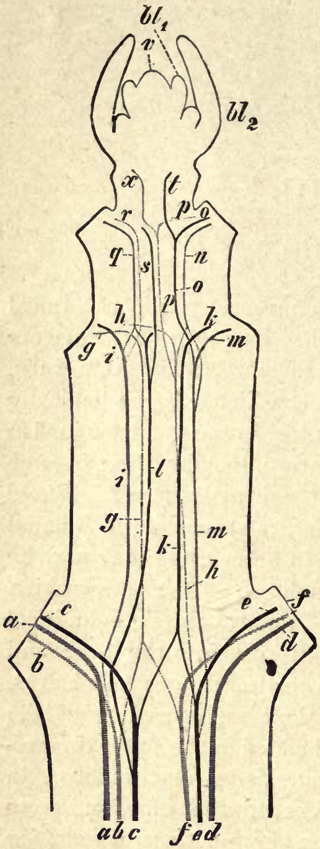


FIG. 20.

Clematis viticella. End of a branch which has been made transparent by the removal of the superficial tissues and treatment with caustic potash. The emerging strands have been slightly displaced by gentle pressure. The two uppermost pairs of young leaves (bl^1, bl^2) are still without leaf traces; *v*, apical cone. (S. after Naegeli.)

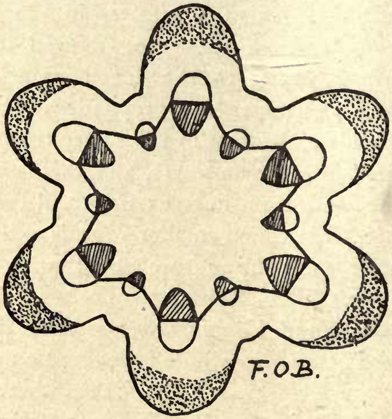


FIG. 21.

Transverse section of an internode of a stem of *Clematis*, showing a ring of six larger and six smaller vascular strands, surrounding the central pith, and covered externally by the thick cortex. The collenchyma massed at the projecting angles is dotted. (× 15.)

for them in the shoots of Dicotyledons. There are differences in the number of the strands entering from each leaf in various examples. In some there is only one strand, in others more. The arrangement of the leaves on the stem may also vary, as well as the distance through which the strands keep a separate course down the stem. Such differences will naturally alter the number and relations of the strands. But as they all regularly take the curved course in the way shown in *Clematis*, the vascular strands will appear in all ordinary Dicotyledons to be arranged in a circle in the transverse section. Within that circle lies the central column of *pith*. Outside it is a more or less broad band of *cortex*, and externally is the *epidermis*. The pith and cortex thus embed the vascular system, and are sometimes called collectively the *ground-tissue*. It is in herbaceous Dicotyledons that these tissues are most easily studied, such as the Bean, Sunflower, or Potato.

Stems of Herbaceous Dicotyledons.

The superficial layers of the stem in herbaceous Dicotyledons show well-marked characters, and are relatively simple in construction (Fig. 22). Starting from the outside, the *epidermis* appears as a

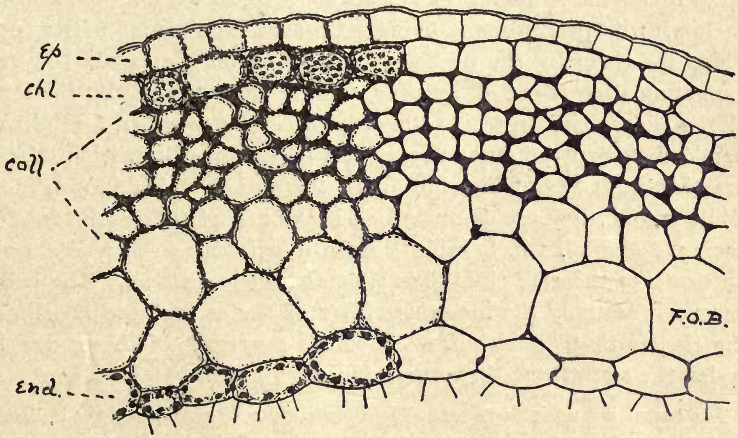


Fig. 22.

Superficial tissues of the stem of Potato. (× 100.) *ep*=epidermis; *chl*=outermost layer of the cortex containing chlorophyll corpuscles. *coll*=collenchyma; *end*=endodermis with starch grains. The protoplasmic contents of the cells are omitted on the right, so as to make the cell-walls appear more prominent.

single superficial layer of living cells, each with its lining of cytoplasm. The outer wall of each cell is thickened, and covered externally by a thin film of *cuticle*, which, being almost impervious to water, controls the loss by evaporation. The epidermis thus forms a skin protective both mechanically and physiologically. It is, however, interrupted here and there by breathing pores, or *stomata*; but none of these happen to have been traversed in the section drawn. They serve for ventilation of the tissues, and will be described later (compare Figs. 45-50).

Beneath the epidermis is a band of *cortex*, limited internally by the *endodermis*, which is the innermost layer of its cells. They are easily recognised while young by the *starch-grains* which they contain (dark blue with Iodine solution). The outermost layer of the cortex consists of thin-walled cells containing green *chlorophyll-grains*, while triangular spaces occur where their walls meet. It is chiefly this layer that gives the green colour to the stem. Beneath it lies a broad band of cells with their cellulose walls thickened at their angles, which gives them added strength. It is called *collenchyma*, and it passes over gradually to an inner, thin-walled cortex, with cells of larger size, and triangular *intercellular spaces*. These spaces are formed by splitting of the cell-walls as they pass from the young to the mature stage, at the angles where they meet. As in life they are filled with gases they form a connected *ventilating system*, which communicates with the outer air through the stomata. The cells of the cortex are all living cells, each with its protoplasmic lining. Gaseous interchange is thus provided for them by the connected system of air-channels. But this communication is cut off inwards, or at least restricted, by the layer of the *endodermis*, in which the cells fit closely together, and form a barrier between the outer tissues and those which lie within. They are thin-walled, and in addition to the starch which they contain while young, they are characterised by a band of corky substance on each radial wall, which being thrown into folds as the wall shrinks on death of the cell, gives the appearance of a *dark dot*. The endodermis is actually the innermost layer of the cortex, and it delimits the tissues that lie within. The whole aggregate of these may be styled the *central cylinder*, or more briefly the *stele*.

The cortex is a variable tissue. The Potato gives an example of the bulk and character that is usual for herbaceous stems, in which the stele is relatively large and the cortex narrow. In young woody stems the stele is smaller in proportion at first, and the cortex usually broader, as it is in *Clematis* (Fig. 21). Aquatic plants have a contracted stele, and the cortex is more bulky still, with large intercellular spaces; as in *Hippuris*, or the Pond Weeds. On the other hand, in some Monocotyledons, and especially in the Grasses, it may be extremely narrow, so that the stele takes up nearly the whole transverse area. It may also vary in constitution. Sometimes it consists wholly of soft green parenchyma, as in *Hippuris:* or this tissue may be associated in various ways with strengthening collenchyma: or sometimes it may be hard and woody, as it is in the haulms of Grasses. It may also contain occasional tissues, such as resin-passages (Sunflower, Ivy, Pine), or milk-vessels and cells (Dandelion and Spurge). But however variable, it is constantly present between the epidermis and the stele.

The stele *comprises the ring of vascular strands, together with the tissues that envelop them, and the central column of pith.* The *pith* is a bulky mass of thin-walled parenchyma, its living cells resembling those of the inner cortex. Similar tissue may

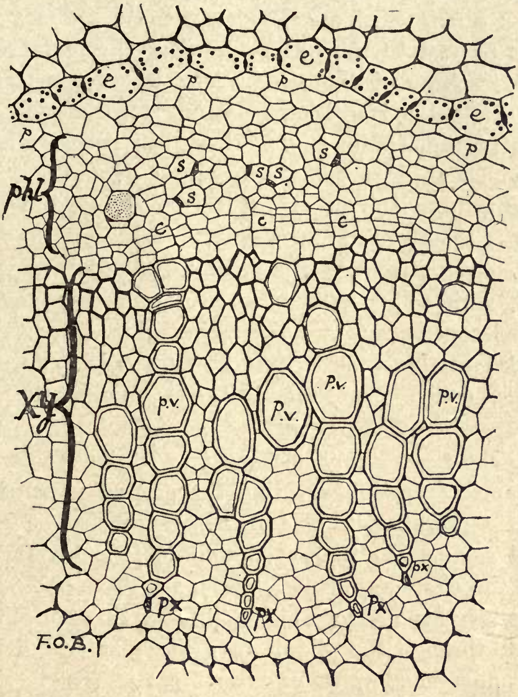


FIG. 23.

Transverse section of a vascular strand of *Scrophularia nodosa*. *e*=endodermis. *p*=pericycle. *phl*=phloem. *s*=sieve-tubes. *c*=cambium. *xy*=xylem. *p.v.*= pitted vessel. *px*=protoxylem. (× 150.)

extend between the vascular strands outwards to the endodermis. A single strand of the stem of the Figwort thus isolated is shown in transverse section in Fig. 23. It is typical of an herbaceous Dicotyledon. The endodermis (*e*), indicated by its starch-grains, defines the inner limit of the cortex. The *vascular strand* is roughly oval in section, but it is not strictly circumscribed. It consists of two main regions which differ in structure and in function. A softer region, which lies peripherally, is called the *phloem*, or *bast* (*phl*); a firmer region, which lies next the pith, is called the *xylem* or *wood* (*xy*).

Between them are very thin-walled cells showing active division; this is the *cambium* (*c*). The transition between this and the wood appears sudden in the drawing; but the radial rows in which the cambial cells are arranged may be traced inwards into the wood, and also outwards into the bast, showing that all the tissues are structurally related.

The most marked constituents of the *xylem* or *wood* are radial rows of *tracheae*, or *vessels* which are elements with thick woody walls. The smallest are nearest to the pith; these are the *protoxylem* (*px*), or first-formed tracheae of the wood. The larger tracheae are *pitted vessels* (*p.v.*), and the transition from one to the other is gradual. There is no protoplasm in any of these, but they are embedded in tissue of which at least some cells retain it, and are thus alive. Near to the protoxylem the tissue is thin-walled, but towards the cambium it is thick-walled and woody, so that here the xylem forms a firm and coherent mass. The *phloem* or *bast* has no woody walls, but is soft, with cellulose walls and protoplasmic contents. The most marked constituents are the rather wide *sieve-tubes* (*s*), which are embedded in thin-walled parenchyma. A layer of more or less definite cells, called the *pericycle* (*p*, *p*) adjoins the endodermis internally.

By seeing the tissues only in transverse section a very incomplete idea is obtained. It is like seeing the ground plan of a building without the "elevation." The tissues must also be examined in longitudinal section, so that each unit is followed throughout its length, and the character of its lateral walls disclosed. If a longitudinal section be taken in a radial plane through the stem of the Figwort, so as to cut through the middle of a vascular strand like that in Fig. 23, its appearance would be as in Fig. 24. To the right are the external tissues, and the pith to the left. Starting from the *epidermis* (*ep*) its cells are oblong, with their outer walls thickened and cuticularised. A *stoma* has been cut through longitudinally (arrow). Below is a thin-walled *cortex*, with intercellular spaces. There is no collenchyma here, and the cortex is a narrow band. It is limited internally by the closely-fitting oblong cells of the *endodermis* (*endod*), with numerous starch-grains, which marks off the cortex from the stele. The *vascular tissue* shows up as a compact strand of more elongated elements, the phloem being thin-walled, and the xylem thick-walled and woody. The *sieve-tubes* are now seen to be long cylinders, traversed here and there by oblique septa of beaded appearance. These are the *sieve-plates* which are perforated, while the cytoplasm that lines the tubes is collected in a mass above each plate. The tubes are embedded in long prismatic cells of the phloem-parenchyma, and in this stem no bast-fibres are present.

The *cambium* consists of long, very narrow cells, with thin walls and dense protoplasm. In each radial row of them the cells are as a rule of the same length, showing that they are the result of division of a single parent cell.

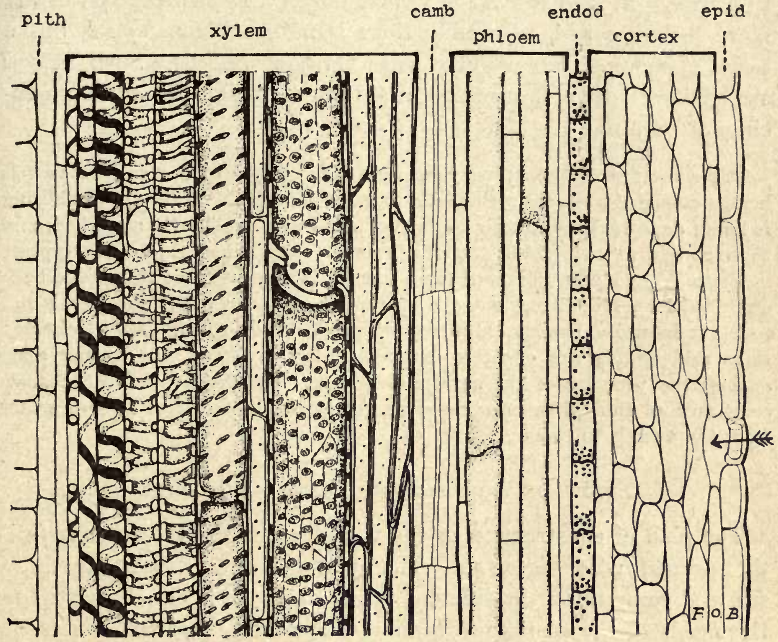


FIG. 24.

Median longitudinal section through a vascular strand of *Scrophularia nodosa*, similar to that shown in Fig. 23. The arrow indicates the pore of a stoma. (× 150.)

The *xylem* is more varied in structure, and if the section happened to have followed one of these radial series of vessels seen in the transverse section, its appearance would be as shown in Fig. 24. Starting inwards from the cambium, a series of *fibrous tracheides* would be met. They are elongated and pointed, with thick lignified walls bearing small pits. They surround and embed a larger *pitted vessel*, which appears as a wide tube without any protoplasmic contents, and is limited by a thick, pitted, woody wall. About half-way down the section it is marked by a ring; this indicates where an oblique septum divided two of those cells from the fusion of which the vessel was derived. That septum was in fact occupied by a large round pit, of which the margin remains as the ring, while the thin pit-membrane has been absorbed. Further inwards the vessels are successively smaller, and show very characteristic markings. In this particular case there is first another pitted vessel, but narrower, with the pits arranged with some spiral indication. In the inner vessels complete *spiral* bands of thickening are coiled within the thin wall. In the successive vessels nearer the pith the spirals are more loosely coiled, till finally there is no continuous spiral, but a series of more or less regular rings (*annular vessels*). Such vessels are characteristic of *protoxylem*, and they abut directly on the parenchymatous pith.

The structure of the protoxylem is a consequence of the earliest vessels being developed while the stem is still growing in length. While the thickening is being deposited upon their walls they are being constantly stretched, and those earliest formed will be stretched most. The annular thickening appears in these. The closer spirals of those formed later show that they have been stretched less. Finally, where the stretching has been slight, the spirals run together laterally, leaving only irregular pits between them. The thickening rings and spirals are effective in keeping the cavity of the vessels open against the pressure of the surrounding cells. On the other hand, a sufficient area of thin pit-membrane is necessary to allow of free exit of water from the vessels to them.

Stems of Aquatic and Climbing Plants.

The plan of construction of the vascular bundle of *Scrophularia* is that *general for Angiosperms*. The bundles, however, vary greatly in size and composition in different types, and this is closely related to the needs of the plants in question. A marked variant is seen in aquatic plants, where the need of water-supply is not pressing. There the woody tissue is reduced sometimes to the vanishing point (*Elodea*); and in less extreme cases the stele is contracted, and the individuality of the vascular strands is not maintained (*Hippuris*). In plants with a climbing habit, on the other hand, the vascular strands are isolated, with bands of soft parenchyma between them, while the wood-vessels are large, and the phloem plentiful. A case in point is seen in the Cucumber (Fig. 25). Here, though the vessels are few, their radial rows can be traced, with the protoxylem directed centrally. A few vessels of enormous size associated with pitted tracheides replace the more numerous vessels of herbaceous stems. The most marked modification is in the phloem, which is much more plentiful. A large mass of it with numerous large sieve-tubes is seen in the normal position; but additional sieve-tubes are present also on the side adjoining the pith. Cambial activity is evident between xylem and the outer phloem, and a few divisions are also seen between the xylem and the medullary phloem.

The stems of climbing plants, and especially of the Cucumber and Vine, have been habitually used to demonstrate the structure of *sieve-tubes*, because there they are specially large. In Fig. 25 the

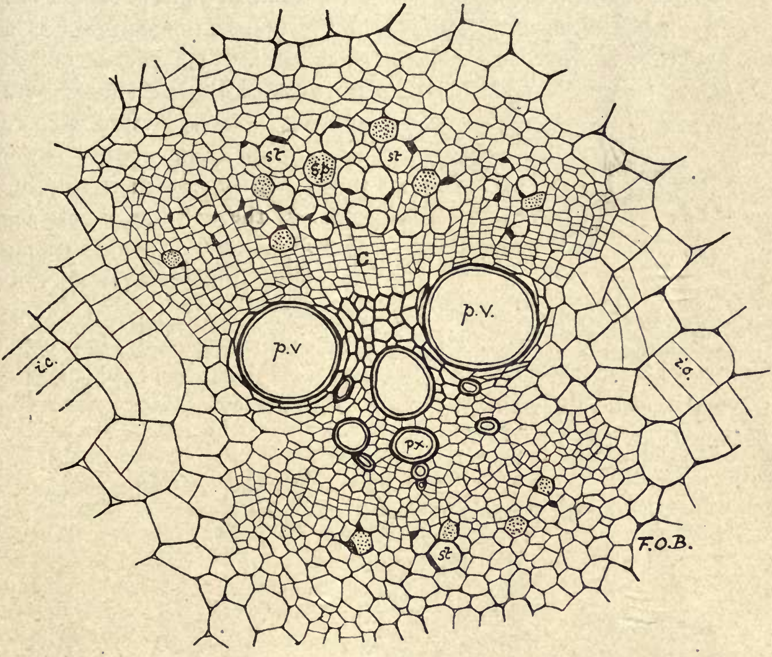


FIG 25.

Transverse section of a vascular strand of the Cucumber, showing plentiful phloem both on peripheral and central sides of the xylem (bicollateral). The vessels of the xylem are few, but very large. *st*=sieve-tubes. *p.v.*=pitted vessels. *px*=protoxylem. *ic*=interfascicular cambium. (× 75).

sieve-tubes appear nearly circular in transverse section; they are limited by a cellulose wall, and a cytoplasmic lining invests the wall during life. This readily contracts from the wall when the tissues are cut across, and the internal pressure relieved. That is the state in which they are usually observed. Associated with each is a small *companion-cell*, often triangular in transverse section, and with dense nucleated cytoplasm. Where a sieve-plate is included in the section it will present a surface perforated by dot-like pores. The contents are densely aggregated round the plate. Under a high power, when treated with solvents that remove the contents, and stained, the structure of the perforated cellulose wall is well seen (Fig. 26). Longitudinal sections show that the tubes are partitioned at intervals by transverse or oblique septa, each of which bears a sieve-plate that occupies its whole area. The cytoplasm contracted in the preparation appears as a thick cord which widens out so as to cover the sieve-area, with which it is closely related. There are no nuclei in mature sieve-tubes. In fine sections suitably stained the continuity of the cytoplasm by threads traversing the pores can be easily seen. But another way of demonstrating the continuity is by treatment with sulphuric acid which destroys the cell-wall, while the more resistant cytoplasm retains its outline (Fig. 28, *D*).

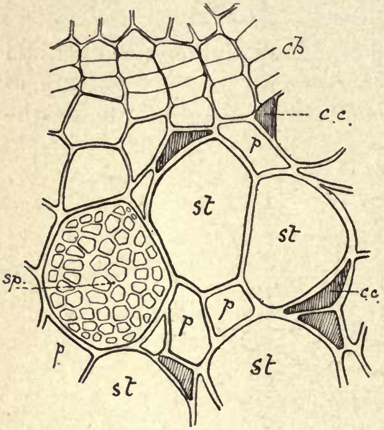


FIG. 26.

Phloem and cambium (*cb*) of Cucumber (× 200). *c.c.*=companion cells. *st*=sieve-tubes cut through between the sieve-plates. *sp*=sieve-plate in surface view. *p*=phloem parenchyma. F.O.B.

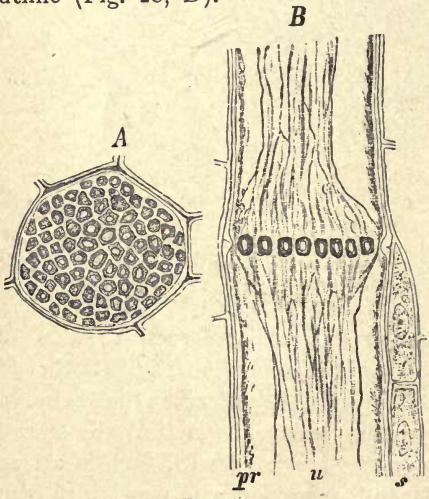


FIG. 27.

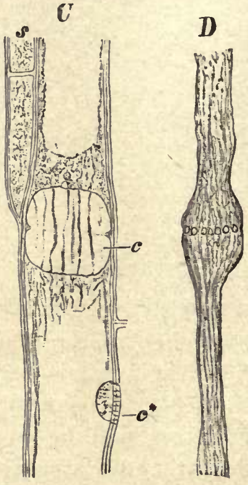


FIG. 28.

Sieve-tubes of *Cucurbita Pepo*. *A*=surface view of a sieve-plate. *B*, *C*=longitudinal sections showing segments of sieve-tubes. *D*=contents of a sieve-tube after treatment with sulphuric acid, showing continuity through a sieve-plate. *s*=companion cells. *u*=mucilaginous contents. *pr*=peripheral cytoplasm. *c*=callus plate. *c**=small lateral sieve-pit, with callus plate. (× 540.) S.

As a tube grows older a mass of *callus* substance is formed around the cellulose framework (Fig. 27, *A*), embedding it and penetrating its pores, so that finally they may be quite closed. In most plants a tube which has been thus closed does not resume its function (*e.g.* Cucumber) (Fig. 28, *C*). But in some cases (*e.g.* Vine) the autumn-formed callus, which is a readily soluble carbohydrate, may be re-absorbed in the spring, and the sieve-tube resumes its activity. The function of the sieve-tubes is for the transfer of the less-diffusible substances, such as proteids. But it is possible that other substances, such as sugars, may also be conveyed by them. The function of the nucleated companion-cells is still unknown. Judging from the constancy of their occurrence it is probably an important one.

The sieve-tubes are sometimes called bast-vessels because of the analogy in development and structure between them and the vessels of the wood. In both cases a number of cells fuse to form the vessel. In the wood-vessel the walls separating these cells are occupied by one or more large pits. As the walls thicken with woody deposits these thin pit-membranes break down, while the original protoplasm is absorbed. The cavities of the cells thus coalesce into a continuous tube, which is filled in life by sap, with or without bubbles of gas. They serve as open channels of transit for water with substances in solution. But the distance through which they are continuous as open tubes is usually limited to a few centimetres.

Similarly the sieve-tubes originate from a number of cells usually attached end to end. The terminal walls bear the sieve-plates, each plate is thickened in a reticulate manner, and the meshes are styled sieve-fields, which are actually individual pits. Each of these is stopped when young by a pit-membrane which is perforated by fine threads. These perforated membranes are then completely absorbed, so that a thick rope of protoplasm replaces the fine threads. Thus the sieve-tube is also a cell-fusion. But at maturity its walls still consist of cellulose; the protoplasts lose the nuclei they originally contained, and the tube is filled with a vacuolated column of non-nucleated cytoplasm, which is continuous through the open pores of the sieve. The analogy of their development with that of the wood-vessels is close, but the contents and the function are different.

Stems of Monocotyledons.

In the Monocotyledons both the arrangement and the structure of the vascular strands may differ from that in the Dicotyledons, though the general plan is essentially the same. The cortex in Monocotyledons is reduced, but the stele is distended, containing isolated vascular bundles, but no cambium. The vascular strands are sometimes disposed in a simple ring round a central pith, as in *Tamus* or *Schoenus*

(Fig. 29). In other cases their regularity is disturbed, the largest of them lying isolated towards the centre. But in sections of Palms,

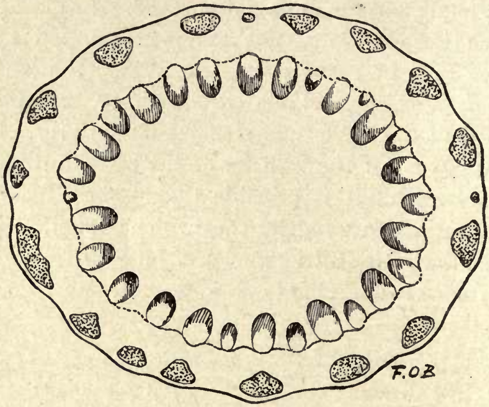


FIG. 29.

Young shaft of *Schoenus nigricans* cut transversely: centrally is the pith, surrounded by an irregular ring of vascular bundles. The dotted patches near the periphery are mechanical tissue. (× 35.)

Maize, and Sugar-Cane such strands appear scattered throughout the pithless stele (Fig. 30). This is a consequence of the fact that

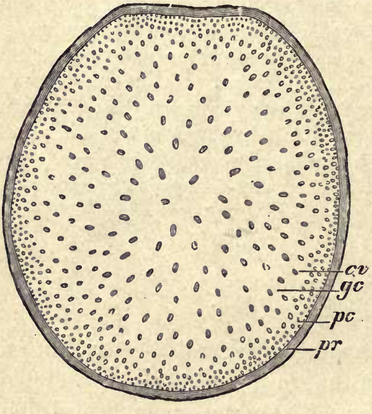


FIG. 30.

Transverse section of an internode of *Zea. Mais.* *pr*=primary cortex. *pc*=pericycle. *cv*=vascular bundles. *gc*=conjunctive parenchyma. (× 2.) S.

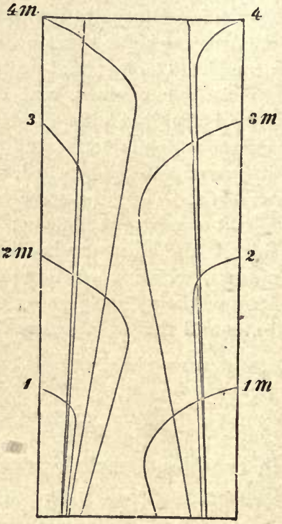


FIG. 31.

Diagram showing the course of the vascular bundles of the "Palm type" of Monocotyledons. The numbers indicate the succession of the alternating leaves. *m*=median bundle. (After De Bary.) S.

each of the largest strands on entering the stem from the leaf slants sharply inwards, but short of the centre it curves again outwards, and gradually approaches the periphery. There it fuses with other strands. As the strand is thickest in the middle of this course, the consequence is that the strands are fewest and largest at the centre, and smaller but more numerous near to the periphery (Fig. 31).

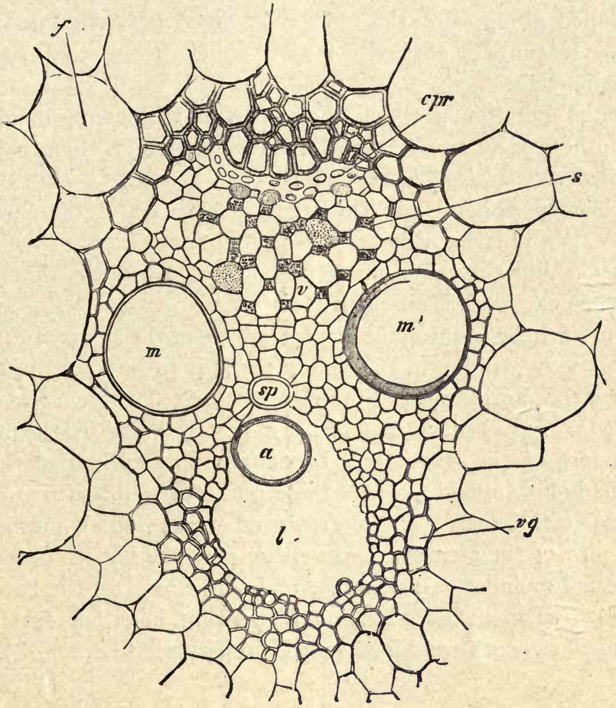


FIG. 32.

Transverse section of a vascular strand from the internode of *Zea Mais*. *a*=annular tracheid. *sp*=spiral tracheid. *m, m'*=vessels with bordered pits. *v*=sieve-tubes. *s*=companion cells. *cpr*=compressed first tissues of phloem. *l*=intercellular space. *vg*=sclerotic sheath. *f*=conjunctive parenchyma. (× 180.) S.

Thus the difference between the arrangement of the strands in Dicotyledons and Monocotyledons is not fundamental. The one type graduates by intermediate steps into the other.

Similarly the structure of the strand itself is on the same plan in both, the most conspicuous difference being the absence of cambium in the Monocotyledons. One of the larger strands towards the centre of the stem of Maize shows features usual in them (Fig. 32). It is embedded in thin-walled conjunctive parenchyma of the stele, and is surrounded by an indefinite sheath of sclerotic fibres. It consists of xylem directed as in the Dicotyledons to the centre of the stem, and phloem towards the periphery. The xylem is represented by two or three annular or spiral vessels of the protoxylem (*a*, *sp*.), adjoining a large air-space (*l*), and two large pitted vessels (*m*, *m'*), with a bridge of fibrous tracheides coupling them together. The number of these vessels may vary, especially near to the nodes. Together they form a **V**-shaped group, and the phloem is fitted between the limbs of the **V**. It consists entirely of sieve-tubes (*v*, *v*), and associated companion-cells.

Vascular bundles in which the xylem and phloem run alongside one another, as in the stems of Dicotyledons and Monocotyledons, are called *collateral*. The xylem is usually directed centrally, and the phloem peripherally in the stem. The case of the Cucumber, where extra phloem adjoins the protoxylem, is described as *bi-collateral*. When a cambium is present the bundle is described as *open*, when cambium is absent it is *closed*.

The uniformity of the cylindrical structure of the stems of Flowering Plants is very striking. The reason for it is to be found in the fact that it satisfactorily meets the requirements. The stem has at once to serve for the physiological transfer of material, and for the mechanical support of the leaves and branches. The cylindrical form, or even the hollow cylinder serves these purposes well. A parallel may be drawn with bones. The marrow-cavity corresponds mechanically to the pith of the stem, while in either case the harder tissue forms an external cylinder. In the case of Birds, however, the bones may be hollow, as in a Grass-haulm. The result in either case is high mechanical strength combined with lightness (see Chapter X.).

Woody Stems of Dicotyledons.

If the apical bud be capable of unlimited growth and production of new leaves, and if in the axil of each there is a bud which may grow into a branch similarly endowed, some further provision must be made for the mechanical and physiological support of the enlarging plant. Particularly will this be necessary in plants which continue growing for a number of years, and thus attain large size. In them the requirement is met by *secondary growth*, through the activity of the tissue called the *Cambium*. It is present even in herbaceous Dicotyledons, but it is specially active in enlarging the trunks and branches of shrubs and trees. From the bulky column thus formed the superficial tissues may be peeled off, separating with special ease in the spring. The line of easy rupture is the *cambium* itself, and the reason why it splits so easily is that in the spring it is actively growing, and its cells are then specially thin-walled and weak. It will be necessary first to examine this tissue in detail, since it produces such important changes.

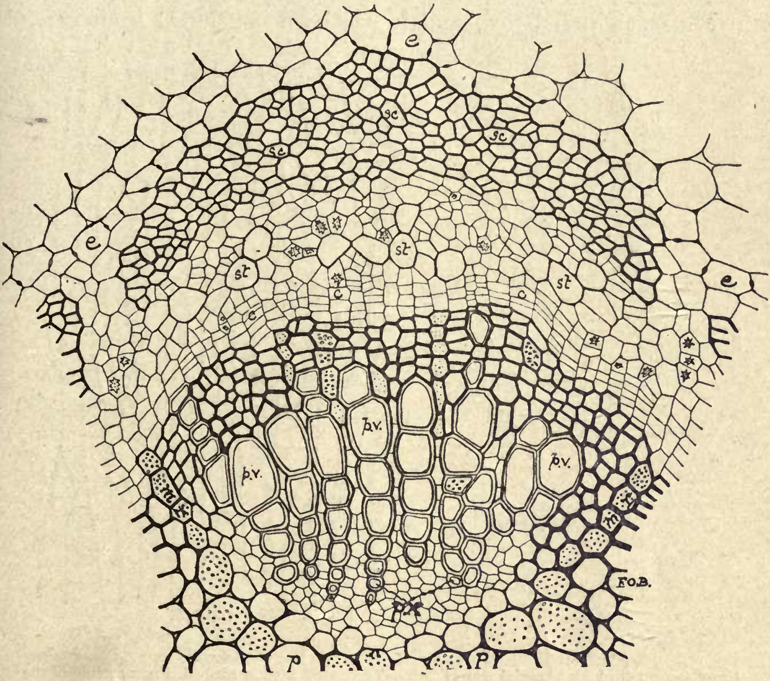


FIG. 33.

Transverse section of a single vascular strand from the young stem of the Elm. *ee*=endodermis. *sc*=sclerotic pericycle. *st*=sieve-tubes. *cc*=cambium. *p.v.*= pitted vessels. *px*=protoxylem. *mr*=medullary rays. (× 150.)

In herbaceous stems of Dicotyledons, such as the Sunflower, Figwort, or Cucumber (Figs. 23, 25), the cambium is seen between the wood and bast of the vascular strands. In woody stems it occupies a similar position, as in the Elm (Fig. 33). The difference is only one of the proportion of the tissues, and of the activity of the cambium. Where the strands are separate, as in herbaceous stems, the cambial activity may be seen to bridge over the spaces between the strands, thus completing the cambial ring. The cambium thus forms a complete cylinder. The parts within the strands are called *fascicular*, and those between them *inter-fascicular cambium* (*i.c.* Fig. 25). In woody stems where the strands are closely grouped, this distinction is not so obvious.

The cambium is recognised by the repeated division of its thin-walled cells by tangential walls, so that *radial rows of cells* are produced. As there is no limit to the repeated divisions, a great increase of the tissues may be the result. The clearest evidence of division is in the centre of each radial row, and it has been concluded from careful

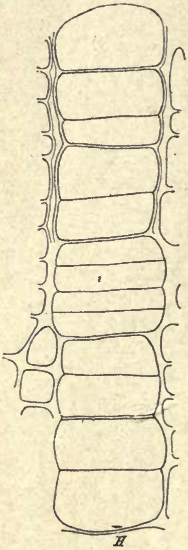


FIG. 34.

Cross section through a radial row of cambial zone in *Pinus sylvestris*, after Sanio. (× 400.) *H*=side next the wood. *i*=the conjectural initial cell. (From De Bary.)

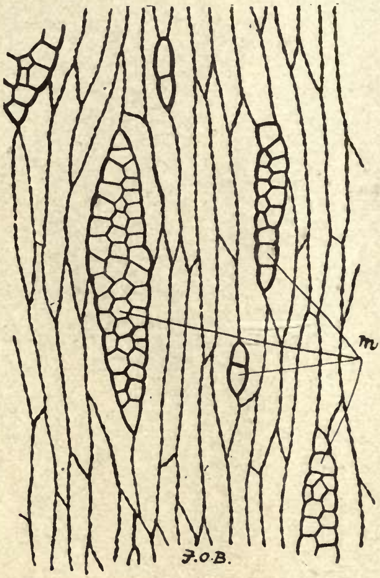


FIG. 35.

Tangential section through the cambium of the Elm, showing the elongated form of the prismatic cambium cells. *m*=the groups of cambial cells forming medullary rays. (× 100.)

comparison of many such rows that in each of them there is an ultimate initial-cell, which retains its identity, giving off on the one side cells formative of wood, and on the other cells formative of bast. This has been styled Sanio's law of cambial division (Fig. 34).

In transverse section each cambium cell appears oblong, with the broader sides facing inwards and outwards, while the narrower run radially (Figs. 23, 25, 33). If a section be taken longitudinally through the cambium in a tangential plane, the cells appear with pointed ends interlocked one with another (Fig. 35). If a radial section be taken, so as to follow one of the radial rows, the individual cells will appear long and narrow, with square ends (Fig. 24). Putting together the results of these three sections, the form of the cell as a solid body would be flattened prismatic; it is placed with

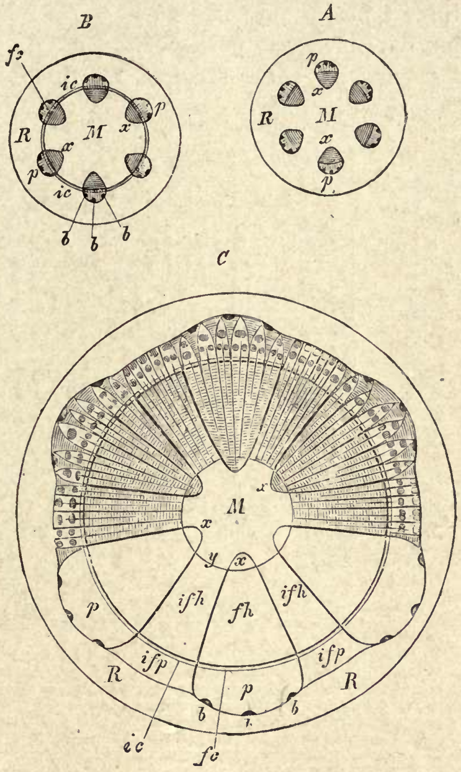


FIG. 36.

Diagrams of secondary thickening in stem of Dicotyledon, based on transverse sections of the hypocotyl of *Ricinus*. *A* represents the stem before origin of interfascicular cambium. *B*, same after it has been formed. *C*, after it has produced internally a broad ring of secondary wood, and externally a narrower ring of secondary phloem. *R*=primary cortex. *M*=pith. *p*=phloem. *x*=primary xylem. *b*=bast fibres at periphery of phloem. *fc*=fascicular cambium. *ic*=interfascicular cambium. *fh*=wood of primary bundle. *ifh*=wood developed from interfascicular cambium. *ifp*=phloem developed from interfascicular cambium. By the intercalation of the secondary tissues the primary bast, *b*, *b*, *b*, is removed some distance from the primary wood *x*, *x*. In *C* the principal medullary rays extend the whole distance through the ring, the secondary rays only part of that distance. (After Sachs.)

its pointed ends directed up and down, and its broader faces inwards and outwards. The cells have very thin walls, and plentiful cytoplasm, with a large nucleus. In fact they show the characters of embryonic tissue. The cells given off from the initial cell, after further division pass over gradually to the mature state, forming additions to the tissues already present. Those which lie internally are added to the wood, those externally are added to the bast outside the ring. If this process be continued, the structure of the stem will become like that shown in Fig. 36, *C*.

There are three different purposes to be served by the growing vascular column, viz. increased power of *conduction*, of *storage*, and of *mechanical resistance*. These are met by three different types of tissue, and though differing in detail, all of these are to be found

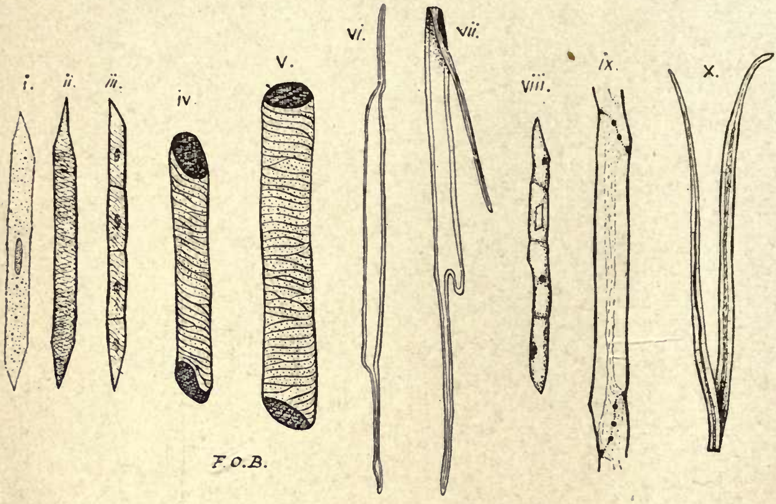


FIG. 37.

Cambium cell of the Lime, and its various products in the secondary wood and secondary bast, all drawn to the same scale, and seen in tangential section. i.=nucleated cambium cell. ii.=fibrous tracheid. iii.=group of cells of wood-parenchyma. iv. v.=single lengths of vessels, the oblique terminal walls having been absorbed. vi. vii.=wood fibres, bent to save space in the figure. viii.=group of bast-parenchyma. ix.=single length of sieve-tube, with oblique terminal walls perforated. x.=bast fibre bent to save space in the figure. (× 75.)

as a rule both in the internal woody column and in the external band of bast. The tissues in question are, the *vessel for conduction*, the *parenchymatous cell for storage* and other functions, and the *fibrous cell for mechanical resistance*. The forms of these various products of the cambial cells, as seen in the stem of the Lime, are shown all to the same scale in Fig. 37, i.-x.

When a large *vessel* of the wood is to be formed, a longitudinal row of cambial cells widen greatly, pushing aside the adjoining cells. The lateral walls become thickened, and usually pitted, but the end walls are absorbed, and the protoplasm disappears. Thus they become tubes for transit of the sap that fills them. As they have lost their protoplasm they are dead elements. Smaller vessels develop similarly, but with less disturbance of the neighbouring cells (iv. v.). When *wood-fibres* are to be formed the cambial cells elongate, and their pointed ends bore their way upwards and downwards, with a sliding readjustment among themselves. As considerable tracts of cells may develop thus alike, and as the cells themselves take a more or less sinuous course, they become interlocked, almost like the strands of a rope. At the same time their walls become greatly thickened, and woody, and their protoplasm disappears. Their function is thus not vital but mechanical (vi. vii.). When *wood-parenchyma* is to be formed the cambial cells widen, and undergo divisions transverse and sometimes longitudinal, into a number of square or oblong cells. Their walls become thick, woody, and pitted, but the cells retain their cytoplasm and nucleus. They are living cells, and are often stored with starch (iii.). Analogous changes occur in the maturing of tissues of the phloem. When *sieve-tubes* are to be formed one or more sieve-plates appear on the oblique terminal walls of the cambial cells; the cytoplasm is continuous through these, and they act as bast-vessels for transit of plastic materials (ix.). The formation and function of *bast-fibres*, if present, and of *bast-parenchyma*, corresponds in essentials to that of the fibres and parenchyma of the secondary wood (viii. x.).

One other component of the vascular column remains to be described, viz. the *medullary ray*. The name is derived from the fact that in transverse section a radial line of tissue, which looks like that of the medulla or pith, runs part or the whole way from the cambium inwards through the wood, and is continued outwards through the bast. Such rays are narrow plates of tissue, and though they may extend far in a radial direction, they are continued only a short distance up or down. They are composed of brick-shaped cells with their longer axis horizontal; these cells have thick pitted walls, and many of them retain their protoplasm and nucleus. They link up with the parenchyma of wood and bast, forming a connected system of living tissue extending inwards and outwards from the cambium (Fig. 38). The rays appear as bright streaks in the mature wood, and are the *silver grain* of carpenters. Two types of rays may be distinguished: *primary rays*, which intervene between the original vascular strands, and extend the whole way from cortex to pith; and *secondary rays*, which are initiated subsequently in the cambium, as the stem increases in bulk. These extend only part way through the vascular ring. The tissue of the rays is derived from special cambial cells, the form of which is best seen in tangential sections (Fig. 35). Such sections also show the outline and relative position of the rays. Triangular intercellular spaces may be seen where their cell-walls join: thus the ventilation-system extends through them deep inwards into the vascular trunk.

In temperate climates the activity of the cambium is interrupted each winter. This leaves its mark on the woody column in the form of *annual rings*, each of which represents the increment of growth of one year. Consequently it is possible by counting them to estimate

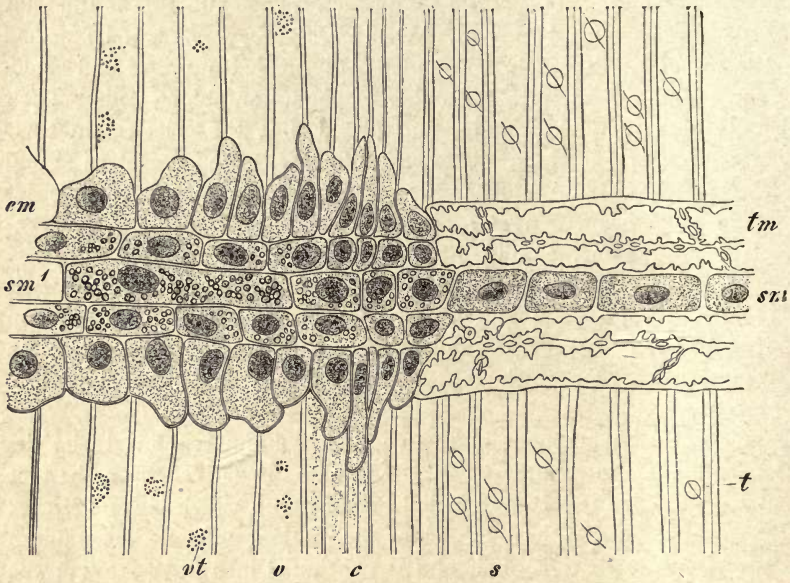


FIG. 38.
Medullary ray of the Pine (*em*, *tm*, *sm*), seen in a radial section through the cambial region (*c*) Phloem to the left, xylem to the right. (× 240.) S.

the age of the trunk. The reason why these rings are recognisable is that the wood formed in the spring has larger and more numerous vessels and on the average thinner walls than that formed as the season advances. The physiological explanation of this is that the first effort of the plant in spring is to increase the water-conducting tissues, so as to supply the new leaves; but in the later part of the season, when nutrition is high, more is spent in thickening the walls, thus adding to the mechanical strength. The result of continued development of a woody trunk in the manner described is to give a column constructed after the plan shown in Fig. 39, where the relation of the annual rings and medullary rays is clearly shown.

As trunks grow old the colour and quality of the central wood changes in many trees, but not in all. It becomes darker in colour, and harder, and it is distinguished as *heart-wood*. It is prized by joiners for its strength and durability, as distinct from the more superficial *sap-wood*, which is paler in colour, softer in texture, and more liable to the attacks of vermin, or fungi, when used in joinery. The change from heart-wood to sap-wood follows on the death of the wood-parenchyma and medullary rays. The sap-wood, as its name implies, is functional for conveyance of sap and for storage. The heart-wood being dead serves only the purpose of mechanical support. It is, however, liable to be attacked by certain fungi in the living tree, which bring

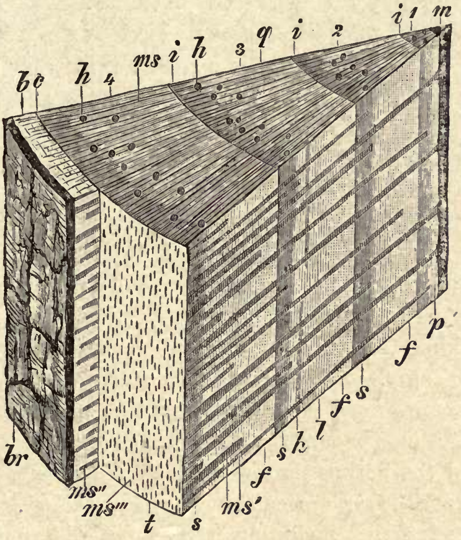


FIG. 39.

Wedge cut out of a four-year-old stem of Pine, in winter. *q*=transverse view; *l*=radial view; *t*=tangential view. *f*=spring, *s*=autumn wood. *m*=medulla. *p*=protoxylem. 1, 2, 3, 4=successive annual rings. *ms*=medullary ray in transverse, *ms′*, *ms″*, in radial, *ms‴*, in tangential view. *c*=cambium. *b*=bast. *br*=bark. (×6.) S.

about its decay. Such hollow trees, though mechanically weakened, retain in their external sap-wood and cambium, and in the more superficial tissues, all that is otherwise necessary for normal life.

The occurrence and proportion, as well as the mutual arrangement of the component tissues are variable in different stems. It is this that gives the characteristic qualities to their wood and bast. Thin walls, and relatively few fibres result in soft wood, as in the Lime. Thicker walls, and numerous fibres grouped in solid masses give a hard wood, like that of the Oak or Laburnum. Fibres may be absent from the bast, as in the Currant; or they may be present in large numbers, forming irregular masses, as in the Lime, which gives the "bast" for tying up garden plants. The grouping among themselves of the several tissues composing the wood and bast appears at first sight confused. To secure conduction, mechanical strength, and storage it is necessary that each of the tissues that meets these needs must be continuous in order to be effective. There is no general or regular rule of their arrangement for all stems. The complex problem is solved by different trunks in different ways. A careful microscopic analysis of the masses of wood and bast is necessary for the understanding of any individual case. But such analysis shows, for instance in the wood, that the three tissue-types form each their own connected system, though all are fused together into the woody column. The clearest example of this is found in the medullary rays, which are intimately related to the parenchyma of wood and bast, and thread together these apparently isolated tracts radially, so as to form a connected living system of storage-cells, which finds its inner limit at the barrier of the dead heart-wood.

The growing vascular column is covered externally as it expands by the cortex and epidermis. These must necesarily yield in some way to the increase within. Sometimes they simply stretch, and this is usual in most stems for a time. But as a rule the epidermis and some of the cortex dries, and peels off, owing to the formation of *cork*. The nature and function of a corky tissue is that it forms an impervious barrier to the passage of fluid. As bottle-cork it is used for this purpose. In the plant a layer of cork, wherever formed, will cut off any tissues outside it from physiological interchange with the tissues within. The first layer may be succeeded by other layers formed more deeply, and cutting off successive bands of deeper tissue. The layers may encroach into the phloem, from which successively the outermost, that is the effete layers, would thus be cut off from the active tissues within. All tissues lying outside the innermost cork-layer are called collectively *Bark*, which is consequently a dead tissue, including it may be epidermis, cortex and phloem. As the stem continues to grow, the bark being dead does not keep pace with it, but splits into fissures, or peels off in scales. Thus the characteristic appearance of the fissured trunks of the Oak or Elm may arise, or the scaly surface of the boles of the Scotch Fir or Sycamore. The thick masses of bark in old stems give also mechanical protection, while they form a non-conducting barrier against excessive heat, as witnessed by the survival of Australian Eucalypts after forest fires.

Cork may originate from the epidermis (Apple, *Sorbus*), but more commonly from the outer cortex, often from the layer immediately below the epidermis (Elm, Birch, Figs. 40, 41). Divisions appear by walls parallel to the outer surface, and are repeated so that from each parent-cell a row of cells is produced. A certain cell in each row remains narrow and thin-walled, and it continues to grow and divide, acting as a cambium-cell. The cells thrown off from it on the inner side take the characters of additional cortex; those on the outer side enlarge, their cell-contents are absorbed, and their

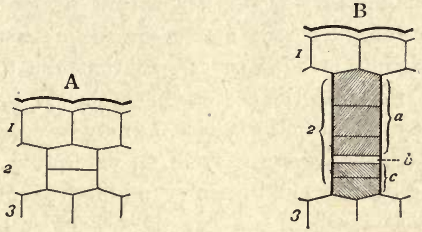


FIG. 40.

Diagrams illustrating successive steps in the formation of cork in the cells (2) directly below the epidermis (1). *A* shows the first division. *B* shows the result of repeated divisions, resulting in a radial row of cells. Of these the outer (*a*) are cork; the innermost (*c*) are phelloderm, which adds to the cortex. (*b*) represents the cork-cambium.

thin walls are changed to impervious cork (Fig. 41: parts right and left of the drawing). As the cells fit closely without intercellular spaces, they form a complete protective covering. Partly owing to the

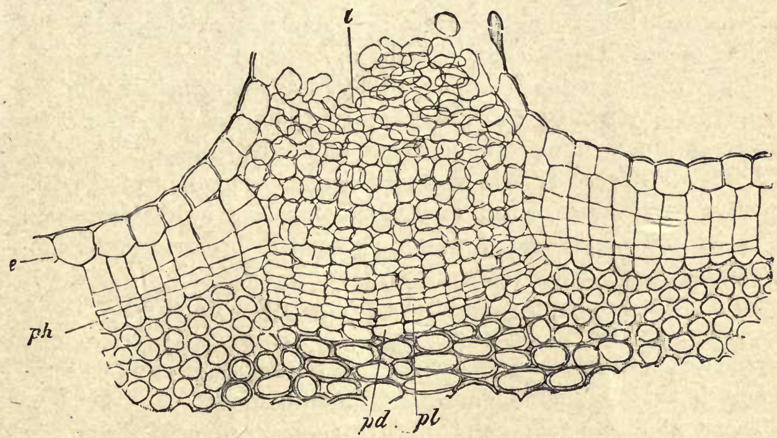


FIG. 41.

Transverse section of the stem of Elder, traversing a lenticel. *e*=epidermis. *ph*=phellogen, or cork cambium. *l*=spongy cells filling the lenticel. *pl*=phellogen of the lenticel. *pd*=phelloderm. (×90.) S.

growth in bulk within, but chiefly because the cork cuts it off from the living tissues, the epidermis soon dries up, splits, and peels away.

The covering of cork having its cells closely fitting together is not only impervious to liquids, but also to gases. Thus the living tissues would be cut off entirely from the outer air, were it not for interruptions of the continuity here and there. These are called *lenticels*, and they may be seen with the naked eye on any stems, as brownish, slightly swollen spots (Fig. 6, p. 13). A lens shows that the epidermis is split, and that powdery tissue lies within. Microscopically it is seen that in place of the closely fitting cork-cells those of the lenticel are rounded, with intercellular spaces, so that the tissue is spongy and allows ventilation into the cortex (Fig. 41). The lenticels remain for years, and may grow to a large size, as may be seen on the surface of many woody trunks, where they often determine the position of the fissures of the bark. The brown crumbling spaces in bad bottle-corks are the lenticels, which traverse the otherwise impervious cork of the Cork-Oak.

The stem of a Dicotyledon showing secondary thickening as thus described is mechanically a stable structure. Its form is that of a cone with its base at the level of the ground. There it often widens out into a broad "stool," which helps to give it stability. Many large trees of the tropics form radiating buttresses at their base, which are still more effective. The stems of Monocotyledons are constructed differently. Most of them do not increase in bulk at the extreme base; but developing stronger above than below, have the outline of an inverted cone, with its apex at the level of the soil. This unstable structure is propped up by roots, which act like oblique struts; as may be very clearly seen in large plants of the Maize, or of the Screw Pine. In many large Palms, however, the base of the stem distends with age. This is due to a general expansion of the conjunctive parenchyma, which may be accompanied by the formation of additional deeply-seated vascular strands. In some few Monocotyledons, however, as in *Dracaena*, there is a cambial increase. It arises in the pericycle, outside the primary bundles, and it forms new vascular strands, which are closed and embedded in a sclerotic parenchyma. Physiologically the result is the same as in Dicotyledons, but it is brought about in a different manner.

Those who have followed the foregoing description of the woody Dicotyledons will see how admirably the trunk meets the requirements. Their shoot-system is constructed on a scheme of indefinite expansion, consequent on continued apical growth and branching. The demands that will be made upon the trunk and branches are well illustrated by any Sycamore or Beech tree exposed to a wind in early summer, after the leaves are expanded and the tree is in full flower. The strain of the wind-pressure is transferred from the leaves to the twigs, and from them downwards to the branches, and finally to the cylindrical trunk. It culminates towards the base, where there is the greatest leverage. The butt must stand firm from whatever quarter the wind may blow. It cannot yield as the branches can without loosening its hold on the ground. Naturally it is here that the trunk is thickest. As it tapers upwards it becomes more pliant; but a condition of successful resistance is the perfect recovery of trunk, branches, and twigs when the wind falls. The *mechanical effectiveness* of the tissues within the several parts is demonstrated by any tree that stands erect and unbroken after a wind.

It is a familiar fact that a detached twig soon wilts by evaporation, and more quickly in a wind than in still air. It requires water in order to recover. In the tree exposed to the wind the young shoots normally retain their firmness. During the wind they will have been exposed to more than normal loss by evaporation, but still they are firm, showing that they have been supplied with sufficient water to make good their loss. The trunk, and the distributing agency of its branches and twigs have carried out their *water-conducting function.* Clearly the water-conducting system meets the requirements.

The rapid production of leaves and flowers in early summer is in itself evidence of the *storage capacity* of the trunk and branches. The material required for their formation is gained previously. The rapid development in the spring depends upon its transfer from the storage tissues in the trunk and branches to the buds that were dormant during the winter. Thus the tree demonstrates by results obvious to any observer the efficiency of the tissues of the trunk and branches for mechanical resistance, water-conveyance, and the storage and transfer of materials. Not only this, but also the method of thickening of the stem is such that it meets the growing demands of the enlarging plant. Finally, the adjustment of the surface tissues to the increasing bulk is peculiarly effective. Not only does the development of cork, and of that heterogeneous covering of bark, give protection to the surface of the increasing stem, but it provides for the removal of effete tissue. The old phloem, with its cells charged with tannin, crystals of calcium oxalate, and many other substances no longer required, together with old and collapsed sieve-tubes, would be a useless burden to the stem. It is cut off by cork, and shed with the decay of the outer layers of bark. The trunk that shows such features as these is highly organised indeed. It is characteristic of those plants which are recognised as the most advanced, viz. the Seed-Bearing Plants, and particularly the Dicotyledons.

CHAPTER IV.

THE LEAF.

EVERYONE knows roughly what is meant by the term Leaf. It is commonly a flat, stalked structure, which exposes a large area of green tissue to the light and air, usually in a more or less horizontal plane; and in a great many of our native plants it falls off in the autumn by detachment at the base of the leaf-stalk. But this general conception of the leaf is not of universal application, and it does not define the leaf in a scientific sense. The essential features of the leaf are not found in its form or direction, or in its detachment in autumn, for all of these are liable to vary. *The features that are constant for leaves, and so define them morphologically, are that they arise as lateral outgrowths from the apical cone, that they spring from the superficial and underlying tissues, and arise in acropetal succession; also that they do not repeat the characters of the shoot itself.* It follows from their origin that their tissues are continuous at the base with the tissues of the axis. The conceptions of axis and leaf are correlative: the axis is a spindle bearing leaves, and the leaf is a lateral appendage upon the axis. Axis and leaves together constitute the *Shoot.* This conclusion holds notwithstanding that both stem and leaf may vary greatly in form and proportion. Particularly the leaf is variable in outline: it may have a stalk or *petiole*, which bears the blade or *lamina* at its end: or there may be no stalk, and the blade is then seated directly upon the axis. Further, the blade itself shows the greatest variety in outline; it may be a simple flat expansion (entire), or it may be cut up in various ways into parts (pinnae), and these may be again subdivided. We need not follow this further than to recognise the fact that the outline of the leaf varies greatly. It may even show differences in the individual, as is seen on comparing the bud-scales and foliage leaves of any ordinary plant with those leaves of the floral region which, however diverse in appearance, are all none the less leaves.

The leaf differs habitually from the stem in its symmetry, though this difference does not apply to all cases, and cannot be held as in itself distinctive of the one from the other. The *stem* is usually *radial* in symmetry, being developed equally all round. But the *leaf* is as a rule a flattened organ, showing what is described as *dorsiventral* symmetry, having more or less clearly defined surfaces. In most leaves one face is turned upwards to the sky, and the other downwards; but this is by no means constant. It is important for clearness of description to distinguish these two faces by some more constant character than that of direction up or down. The most constant is their relation to the axis which bears the leaf. One of the faces is directed in the young bud towards the axis which bears it; it is therefore defined as the *ad-axial*, though as it is usually directed upwards it is often called the *upper* surface. The other faces away from the axis in the bud, and is defined as the *ab-axial*, and as it is usually directed downwards it is styled the *lower*. But the terms "upper" and "lower" are merely descriptive of position: they are not scientific definitions as the others are. The Common Garlic shows how necessary this precision is, for in most of its leaves, by a twist of the leaf-stalk, the ad-axial face is turned downwards.

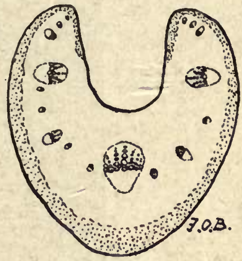


FIG. 42.
Transverse section of the petiole of the Sunflower. (× 6.)

Since the tissues of the leaf are continuous at the base with those of the stem, the constitution of the *petiole* may be expected to resemble that of the stem. But its form is more or less flattened or channelled on the upper (ad-axial) surface. This is in accordance with the mechanical requirements; for it has to support the weight of the blade, and hold it with some degree of firmness in its horizontal position. The necessary strength is secured by a form which in transverse section would appear semicircular, or semilunar, as it is in such a leaf as the Sunflower (Fig. 42). In this case it is traversed by three large vascular strands, which with some smaller strands are arranged in a semicircle. The surrounding tissues are essentially like those of the young stem, but there is no stelar tract defined by a general endodermis; here each strand is surrounded by its own sheath. Naturally the *xylem* of each strand as it curves out from the stem is directed *upwards* (ad-axial), and the *phloem downwards* (ab-axial), and these relative positions are regularly maintained throughout the leaf. The petiole appears to be structurally little more than a means of junction between the axis and the blade. Its presence brings two advantages: that the blade is carried some distance outwards from the stem, and thus the probability of one leaf overshadowing another is avoided; and secondly, the narrow petiole allows the blade to yield to the pressure of wind, instead of rigidly resisting it.

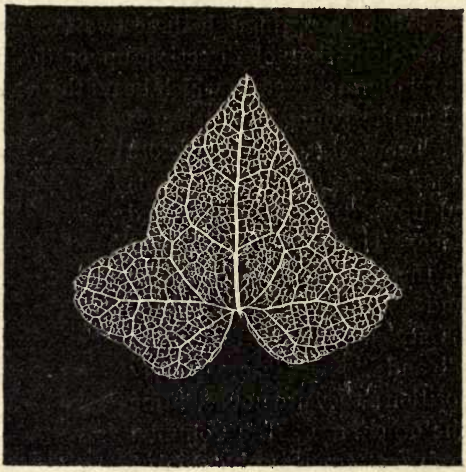


FIG. 43.
Skeleton of the lamina of Ivy. Natural size.

It is the blade, or lamina, which is the distinctive feature of the foliage leaf. As shown in such common types as the Sunflower, Dahlia, Cabbage, or Sycamore, the blade consists of a skeleton or framework of thickened and mechanically firm ribs, which support an expanse of relatively thin and delicate tissues. A prominent mid-rib runs up continuously from the leaf-stalk to the tip of the blade, and branch-ribs of successively smaller size pass off from it towards the margin. On removing the softer tissues by reagents, the vascular system can be demonstrated as a leaf-skeleton (Fig. 43). It is then seen that vascular strands of the midrib and of the stronger lateral ribs, give off thinner lateral branches; that smaller branch-veins pass off from these, and with further ramifications and many fusions form a fine network traversing the thinner areas of the blade. Such a *reticulate venation* is characteristic of the leaves of Dicotyledons. In Monocotyledons the main veins run *parallel* to one another, but still they are connected laterally by transverse branches. Thus the vascular system, of which the leading function is conduction, is very effectively placed for carrying out its purpose. For it is connected below with the conducting system of the stem, and it spreads throughout the blade, and reaches to its extreme tip and margin.

A superficial examination gives only a very imperfect idea of the structure of this important part of the plant. Transverse sections

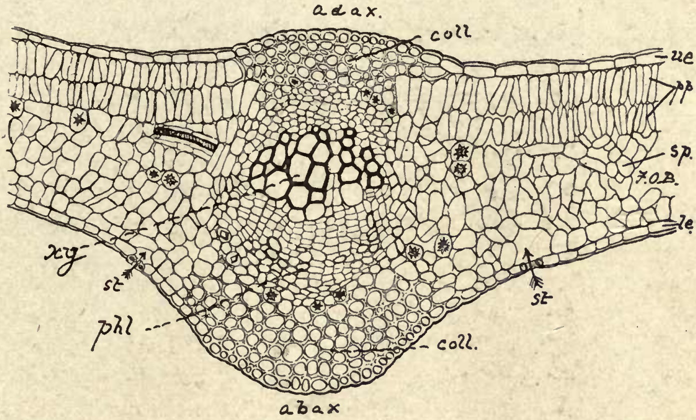


FIG. 44.

Transverse section of the midrib of the leaf of Aspen (*Populus tremula*), extending to the thinner expanse of the blade right and left. *ue*=upper epidermis. *le*=lower epidermis. *pp*=palisade parenchyma. *sp*=spongy parenchyma. *coll*=collenchyma. *xy*=xylem. *phl*=phloem. *st*=stoma. Note numerous crystals of calcium oxalate. *adax*=adaxial or upper, *abax*=abaxial or lower leaf surface. (× 75.)

through the thin *lamina* so as to traverse one of the ribs transversely, reveal the characteristic structure upon which the functional activity of the foliage leaf depends (Fig. 44). The upper (ad-axial) face is easily distinguished from the lower (ab-axial) by the fact that the larger veins project strongly from the latter surface. Where the vein is traversed it shows on a reduced scale the same construction as the petiole, and like it the ribs are often strengthened by collenchymatous tissue, as is seen in the Aspen. Here again the xylem of the vascular bundle is directed towards the upper (ad-axial) face, and the phloem towards the lower (ab-axial). The tissues which compose the thinner expanse of the lamina bear definite relations to these opposed surfaces, and to the incidence of light upon that which faces upwards. They will be described, starting from the upper (ad-axial) face, as they might be seen in the leaf of the Aspen, or as shown more in detail in the Privet (Fig. 45).

The upper surface is covered by a continuous layer of *epidermis*, composed of oblong cells with their outer wall thickened and cuticularised. The lower surface is similarly covered by epidermis, but the cells are less regular, while their continuity is here and there interrupted by pores (*stomata*), which allow communication between the outer air and the intercellular spaces within. Between these two epidermal layers lies the tissue of the *mesophyll*. Towards the upper surface its cells are arranged with some degree of regularity, frequently in

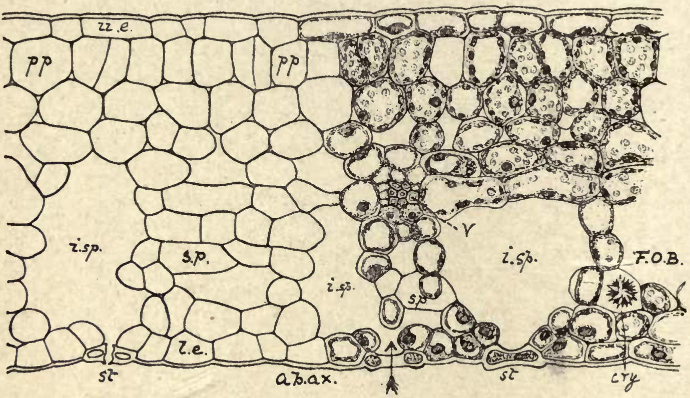


FIG. 45.

Transverse section of lamina of Privet (*Ligustrum vulgare*). *ab.ax* = the abaxial or lower surface. The protoplasts are omitted on the left hand side. *u.e*=upper epidermis. *l.e.*=lower epidermis. *i.sp.*=intercellular space. *v*=vascular strand. *st*=stoma. *pp*=palisade parenchyma. *s.p.*=spongy parenchyma. *cry*=crystal. (×75.)

two layers. The cells of these layers are of oblong form, and stand parallel with one another, the ends of the outermost layer abutting on the epidermis. From their form and arrangement they are called the *palisade-parenchyma*. Towards the lower surface the cells are less regular in form and arrangement, and as the intercellular spaces are very large and numerous this tissue is described as the *spongy parenchyma*. The whole mesophyll is composed of thin-walled cells, with living cytoplasm, a nucleus, and very numerous discoid, green *chlorophyll-corpuscles*. To these is due the full green colour of the leaf. The *intercellular spaces* so conspicuous in the spongy parenchyma, are continuous, though of smaller size, between the palisade-cells, and they connect with the stomata. A specially large space is usually present opposite the pore of each stoma. The whole mesophyll is thus permeated by a ventilating system of air-channels, which may communicate through the pores of the stomata with the air outside.

Most foliage leaves have such a structure as that described. But the leaf-blade of different plants fluctuates almost as much in the details of its internal construction as it does in its outline: this may even be seen in some degree in those of the same individual plant. Leaves may vary in thickness from the delicate, almost filmy leaf of shade-loving plants, to the leathery texture of those exposed to the sun in dry climates. The leaves may be smooth in surface, as is usual in water-plants, or covered with rough hairs like the Sunflower, or with a dense woolly protection like the Alpine Edelweiss. Internally they may have only a single layer of palisade parenchyma, as in most shaded leaves; or two, which is common in leaves exposed to the full sun; or more. They may be strengthened by mechanically effective tissue, often placed just below the upper epidermis (hypoderma), as in the leathery Cherry-Laurel, or distended by water-storage cells, usually occupying the middle of the leaf, as in the succulent Stonecrop, or Aloe. Notwithstanding such differences as these, and many others, the construction is as a rule based upon the same essential scheme as that described.

The leaf is the chief organ of nutrition in green plants. An essential point of structure to this end is the perforation of the epidermis by the stomatal pores, for this gives the opportunity of gaseous interchange between the intercellular spaces and the outer air. *Stomata* occur here and there in the epidermis of the stem and petiole, and even upon the various parts of the flower. But it is on the surfaces of the leaf-blade that they are found in the greatest numbers. Sometimes, as in the Sunflower and many herbaceous plants, they are present on both sides of the blade; but frequently they are fewer on the upper epidermis, or even absent, as in many woody plants. They are often very minute, especially in the Dicotyledons, so that large numbers, usually 100 to 300, may be counted on each square millimetre of surface. The following table gives the result of countings per sq. mm. on the leaves named:

	Upper.	Lower.
Lilac	100	150
Oak	0	346
Apple	0	246
Water Lily	460	0 (submerged).
Wheat	47	52

Examined microscopically in surface view the epidermis of a Dicotyledon appears as a film of tabular cells, often with sinuous outline (Fig. 46). The stomata form part of the epidermal layer, but their cells differ in form from the rest. Each stoma is composed of two *guard-cells* attached by their ends, so that between them there is a pore that may be either open or closed. In a microscopic preparation of a living epidermis taken on a sunny day, and mounted in water, the pores, governed by the still living cells, will be seen to

FIG. 46.

Part of the lamina of *Tropaeolum*, seen as a transparency, in surface view from above; showing the sinuous outline of the epidermal cells, with stomata. Below the palisade-cells are seen end-on, with large intercellular spaces, especially below the stomata. The vascular veins are more deeply shaded. (× 175.)

be widely open, as they are represented to be in the drawing of the leaf of *Tropaeolum*. Access is thus readily given to the intercellular spaces within. Fig. 46 further shows the mesophyll visible through the transparent epidermis. The palisade-cells are here seen end-on; and it is more apparent than in transverse section how well ventilated this tissue actually is. Almost all its cells touch another cell laterally; but in all of them a very considerable proportion of the wall-surface is freely exposed to the gases contained in the intercellular spaces. These spaces are specially large in the neighbourhood of the stomata. Lastly, part of the vascular network is shown dimly in a still lower plane. The strands lie between the palisade and the spongy parenchyma, and the conducting system is thus in near relation to the bases of the oblong palisade cells.

In the Dicotyledons the stomata are relatively small, and irregular in their orientation. They are shown in section in Figs. 44, 45, and in surface view in Fig. 46. In Monocotyledons they are usually larger, and their orientation regular. The large stoma of *Narcissus* serves as an example (Fig. 47). Its guard-cells have a characteristic outline, each with a projecting ridge on its oblique outer and inner walls. The stoma is here slightly sunk below the outer surface of the leaf. The level of the stoma relatively to the leaf-surface varies in different types according to their habitat. In plants of temperate climates

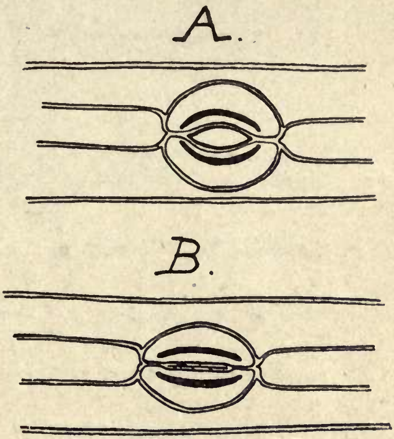


FIG. 47.
Drawings from the same Stoma of *Narcissus*, in surface view. *A*, in the open; *B*, in the closed state. F. O. B. (×250.)

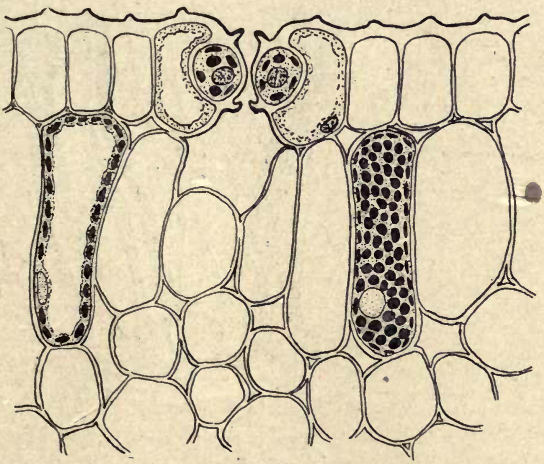


FIG. 48.
Stoma of *Narcissus* in transverse section, showing its relation to the adjoining epidermal cells and to the mesophyll below. Two of the cells of this tissue are drawn in in detail, that to the right as seen in surface view from without; that to the left in optical section. The chloroplasts are black. (× 300.) F. O. B.

it sometimes projects, or lies about level with the general surface. But in plants of dry climates it is apt to be sunk inwards. This

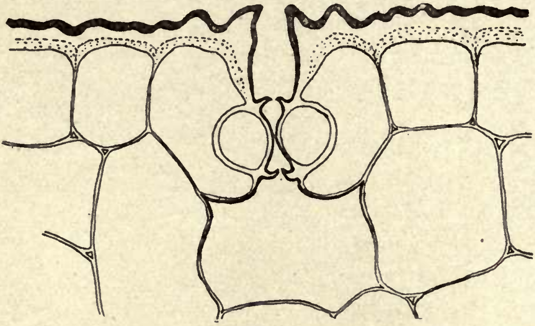


FIG. 49.
Stoma of *Aloe* depressed below the well-developed epidermis. The well-developed cuticle is shown black. (× 300.) F. O. B.

is seen in slight degree in *Narcissus* (Fig. 48), but more distinctly in *Aloe* (Fig. 49), a succulent plant with strongly cuticularised

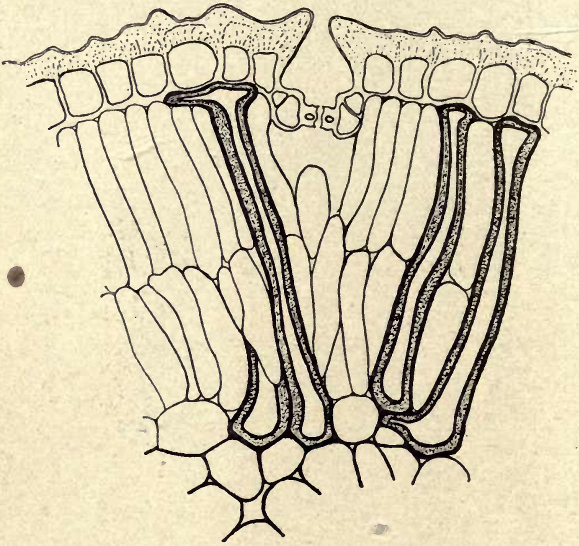


FIG. 50.
Part of a transverse section of the xerophytic leaf of *Hakea*, showing a stoma greatly depressed below the well-developed, and cuticularised epidermis, which is propped out by thick-walled sclerotic cells. (× 150.) F. O. B.

epidermis. The stomata themselves are of the same type as *Narcissus*, but seated at the bottom of deep pits. A more extreme case is seen in *Hakea* (Fig. 50). Additional control over evaporation of water is gained by this means.

Seeing that the epidermis serves for protection, and for regulating the ventilation of the leaf, both functions of a secondary character, it seems clear that the mesophyll is the tissue of prime importance. The cells of the palisade-parenchyma are oblong in form, and each is bounded by a thin cellulose wall, which is rounded off at the angles so as to provide the intercellular spaces (Fig. 48). The cell-wall is lined internally by a film of cytoplasm, within which is a large vacuole filled with sap. The nucleus may be suspended in the middle of the cell, but more frequently it is embedded laterally in the cytoplasm. The most marked features of these cells are the *chlorophyll-corpuscles*, or *chloroplasts*, which are discoid in form and of a full green colour. They are always embedded in the cytoplasm, and are as a rule so placed that one flattened side faces to the cell-wall, the other to the central vacuole. The cells of the spongy-parenchyma resemble the palisade cells in all essential points except in their form, which is very irregular, and in the fact that their chloroplasts are fewer (Fig. 45).

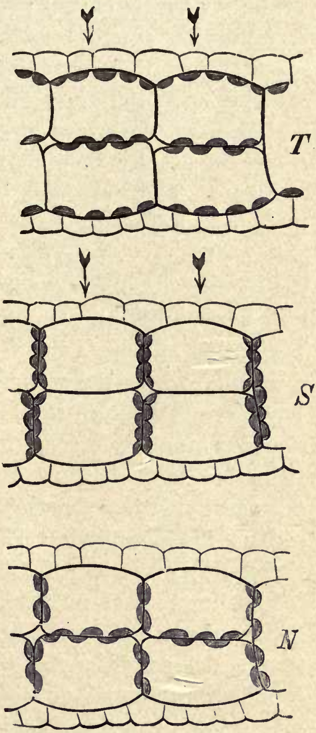


FIG. 51.

Varying positions taken by chlorophyll grains in the cells of *Lemna trisulca* under illumination of different intensity. *T*, in diffuse daylight. *S*, in direct sunlight. *N*, at night. The arrows indicate the direction of the light. (After Stahl.) S.

As the cytoplasm has been seen to be capable of movement, it can alter the position of the chloroplasts embedded in it. Apart from any other disturbing cause, they collect at the cell-surfaces adjoining the intercellular spaces. Their movements are regulated by external conditions, of which one is the aeration of the cell. Another, and apparently a stronger influence is light. In diffused light they place themselves so as to present their flattened surfaces to the incident rays (*T*, Fig. 51); in intense sunlight they present their edges, and so protect themselves from its harmful effects (*S*, Fig. 51).

The origin of the chloroplasts is primarily from the plastids of the embryonic cells, which enlarge and assume a green colour. These plastids multiply by fission, and it is easy to see that the chloroplasts do the same. Comparison of a number of them shows some with an elongated form, others with a median constriction, and others again grouped in pairs as though resulting from a recent fission. As they have never been seen to arise *de novo*, it is concluded that *all the chloroplasts have descended by fission from pre-existing chloroplasts, or plastids.* (See Fig. 72, *B*.)

The structure of the palisade-parenchyma, with its oblong cells, is admirably suited to accommodate large numbers of the chloroplasts, which thus present for the most part their edges to the light incident upon the upper surface of the leaf. The cells of the spongy parenchyma, with their irregular form, are less specially fitted for this, and usually they contain fewer chloroplasts than those of the palisade. They are also less important in that they get most of their light at second hand, that is, after it has passed through the palisade tissue. About midway between the upper and lower epidermis the smaller vascular strands of the reticulum may be found traversing the mesophyll, and in intimate relation with it (Figs. 44-46). They vary in complexity from considerable bundles downwards to a minimum, where the xylem may be represented by a single tracheid. The sieve-tubes stop short before this point is reached; but certain richly protoplasmic cells, like large companion cells, extend further than they towards the vein-endings. Each strand is surrounded by a parenchymatous sheath, the cells of which are in contact with the cells of the mesophyll. Thus the conducting system penetrates and thoroughly permeates the green tissues of the lamina.

The function of nutrition carried on by the green tissues will be discussed more fully in Chapter VII. Here it may be stated simply that under conditions of light and suitable temperature, and when supplied with water and certain salts in solution, *the cells containing chlorophyll, using the carbonic acid of the air, form new organic compounds that serve as food for the plant.*

In the leaves of many plants the period of this activity is limited by the season, and autumn with its lowering temperatures and shortening days leads to the *fall of the leaf.* At the base of the petiole a band of corky tissue is formed in a transverse plane. Immediately above it the cells become rounded off by increase of the intercellular spaces. This is called the *abciss layer*, because the line of fracture is determined by the weakness of its cells, and it is here that the leaf falls away. *The scar is covered by the layer of protective cork*, while the vessels and sieve-tubes running up to its surface are constricted by the pressure of the adjoining cells (Figs. 6, 52). Thus the fall of the leaf causes no open exposure of the living tissues liable to attack by intrusive organisms. Prior to the fall of the leaf its tissues are depleted of all useful materials, which are transferred down the petiole to the axis. This is accompanied by changes in the cell-contents which give the varied autumnal tints. What falls away is then little more than an empty skeleton. Its removal leads to a great reduction of the exposed surface of the plant, with the result that there is less loss from evaporation; and less resistance to the winter winds. As a whole the plant enters a dormant condition in autumn, partly determined by the climatic conditions, partly by the absence of those organs which play so active a part in its vegetation. But the fall of the leaf is not an inherent feature in any group of plants, nor does the abciss layer form any constant limit between leaf and stem. For example, the British Oak (*Quercus robur*) is *deciduous*, that is, it drops its leaves in autumn; but the Holm Oak (*Quercus Ilex*), which is a native of the Mediterranean region, remains *evergreen*. The common Cherry (*Prunus cerasus*) drops its leaves in autumn; but the Cherry Laurel (*Prunus lauro-cerasus*) is evergreen. Thus though the leaf-fall is a very striking feature of many trees and shrubs in temperate climates, it is really nothing more than a seasonal, and often a specific, adaptation. In many woody plants it does not occur at any regular intervals, while in most herbaceous plants, and especially in annuals such as the Sunflower or Bean, the whole shoot simultaneously ceases its vegetative activity, leaf and axis remaining connected till they rot.

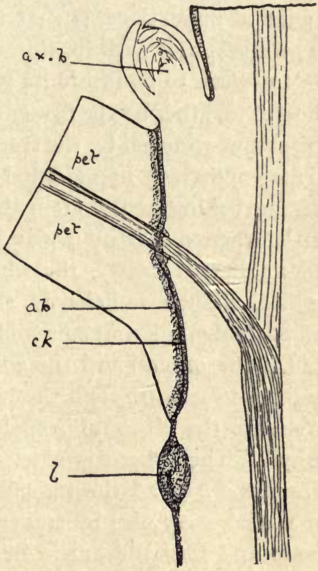


FIG. 52.

Vertical section through the base of a petiole (*pet*) of a Horse-chestnut at its junction with the axis, showing the abciss layer (*ab*) with cork (*ck*) beneath it. (*l*) = a lenticel. When the leaf falls the scar is protected, and the axillary bud (*ax. b*) is left attached. F. O. B. (× 10.)

From the description which has been given of the structure of the leaf it will be seen how well that organ is fitted for carrying out the duty of nutrition, while exposed to the ordinary climatic conditions. In the first place a broad expanse of green tissue is required, so as to intercept the light. The larger its area the better. This is a sufficient reason for the existence of the wide-spread blade. The active cells are those of the mesophyll, and it is essential that their thin cellulose walls, saturated with water, shall be exposed for aeration. But if simply and directly exposed to the atmospheric air they would quickly dry up and shrivel. They are therefore protected on either side by the epidermis, which is a continuous layer covered by the impervious cuticle. Access to the atmosphere is still maintained, though under control, through the numerous stomata, and it extends onwards to the individual cells by means of the intercellular spaces. Another point of importance is that the epidermis gives mechanical strength. The mesophyll with its thin walls and spongy texture would by itself be too weak to maintain its form, and resist the impact of winds. It is bound together by the firmer epidermis. The thin expanse of the blade is further stiffened by the framework of the midrib and veins. (Fig. 43.) These illustrate in modified form the same methods of mechanical strengthening as the stem itself. (Figs. 42, 44.) Often the blade is strengthened also by a marginal band of hardened tissue, which acts like a hem. Lastly, the whole lamina is attached to the leaf-stalk, which, though sufficiently rigid to support it, will yet yield to the impact of wind, and so avoid the risk of mechanical damage.

On the other hand the conducting system is continuous from the axis outwards through the leaf-stalk, and on through the midrib and veins to the ultimate branchlets which ramify throughout the mesophyll. Thus there is efficient provision for the transit of material from the axis to the remotest points of the lamina, and conversely materials may also be transmitted backwards from these to the leaf-base and into the axis. Such transit does actually take place, the first through the woody tract of the vascular strand, the other through the bast. In short, a foliage leaf is fundamentally a structure with adequate provision for mechanical strength, and for the transit of materials backwards and forwards between the axis and its distal points, which is secured by its conducting system: while it exposes as large an area as possible of green tissue to the light, with ready access to the atmospheric air.

CHAPTER V.

STRUCTURE OF THE ROOT.

THE origin of the primary, or tap-root from the radicle of the embryo, the development of the root-system from it, and the relation of that system to the shoot in the normal Flowering Plant have been

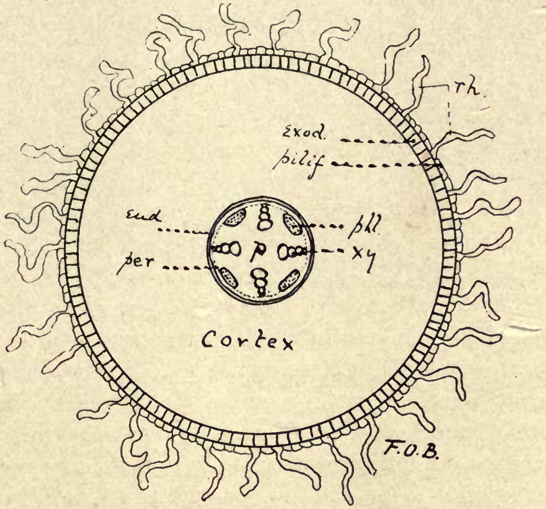


FIG. 53.
Diagram illustrating the arrangement of tissues in the transverse section of a root. *rh*=root-hairs. *exod*=exodermis. *pilif*=piliferous layer. *end*=endodermis. *per*=pericycle. *xy*=xylem. *phl*=phloem. *p*=pith.

described in Chapter I. Its fixation in the soil by means of its root-hairs has also been noted. The details of its structure will now be examined, so that the facts may serve as an introduction to the study of the functions which the root has to perform.

The root is typically cylindrical, and accordingly its transverse section will be circular. The general arrangement of the tissues, exposed in a section cut about two or three inches behind the apex of any ordinary root, is more regular than that usual in stems. It is shown diagrammatically for a thin root, such as that of a Pea seedling, in Fig. 53. There is a superficial covering which may be held as corresponding to the *epidermis*. Within it lies the *cortex*, and centrally the *stele*. But here the cortex is relatively bulky, while the stelar column is much more contracted than is usual in stems. This disposition of the tissues is typical for roots at large.

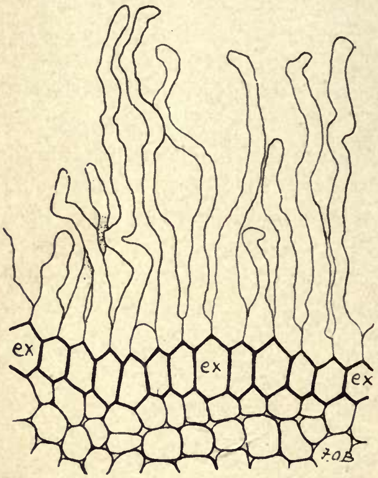


FIG. 54.
External tissues of the root of *Ruscus*, showing each cell of the piliferous layer grown out into a root-hair. *ex*=exodermis. (× 100.)

The superficial layer consists of an unbroken series of thin-walled cells, without any cuticle upon their outer walls. It is called the *piliferous layer* because many of its cells are extended outwards as *root-hairs*. (Figs. 53, 54.) Below the piliferous layer comes the bulky tissue of the cortex, of which the outermost and the innermost layers are sharply defined, while the massive band of tissue between them consists in the young root of a featureless, thin-walled parenchyma with intercellular spaces. The outermost layer, lying directly below the piliferous layer, and with its cells alternating with these, is called the *exodermis*. Its cells fit closely together, and they show a sharply defined corky band upon their radial walls, which often extends with age to the other walls (Fig. 54). This prevents leakage of water outwards, and throws the control of its passage upon the protoplasts of the living cells so long as the root is young. The exodermis is thus a living physiological barrier. Much the same is the case with the innermost layer, which is called the *endodermis*. Its cells also are in close lateral relation one to another, and the radial walls have also a corky band which serves a similar purpose. The cortex thus composed forms the larger part of the area of transverse section, and it may be regarded as a water-reservoir round the stele, controlled both on its outer and its inner surfaces by the protoplasm of living cells.

The most prominent tissues of the stelar column are certain well-defined strands of xylem and phloem. In small roots like those of the Cress or Onion there may be only two of each of these; and the strands may meet at the centre, there being no pith at all. In larger roots of Dicotyledons there are usually more of them, four or five being common numbers (Fig. 56). But the number is not constant in roots of the same species, or even of the same individual. In Monocotyledons the number is usually larger still, and it may run to a very high figure

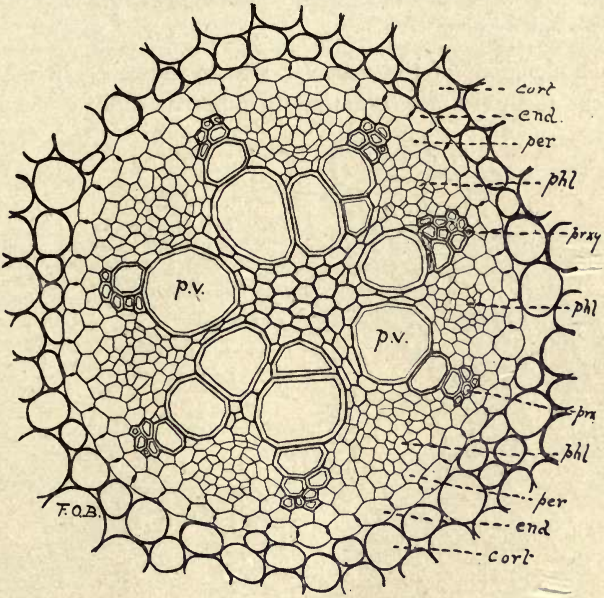


Fig. 55.

Transverse section of the stele of the root of *Acorus*—a Monocotyledon. *cort* = cortex. *end* = endodermis. *per* = pericycle. *phl* = phloem. *prx* = protoxylem. *p.v.* = pitted vessel. (× 150.)

in roots of Palms, or Screw Pines. In such roots a pith is present, and it may be of considerable bulk. A typical structure of the stele for a simple Monocotyledon is seen in the root of the Sweet Rush, *Acorus* (Fig. 55). The cortex and endodermis surround the stele itself, of which the superficial layer is the thin-walled *pericycle*, here a very regular row of cells. There are seven groups of xylem, and seven of phloem alternating with them. Each group of xylem is composed of smaller vessels of the *protoxylem* (*prxy*), which are directed to the periphery, while successively larger, pitted vessels (*p.v.*) constitute the later-formed *metaxylem*. The alternating groups of phloem are not strongly developed, and the whole is compacted by cells of the *conjunctive parenchyma*, which fill up the interspaces and extend to the centre. Here its cells instead of forming a soft pith become sclerotic with age, so that the lignified tissues are all welded together into a central, mechanically resistant strand.

Internally to the phloem cell-divisions may be seen at several points in the Fig. 55. These are in the position where in other roots a cambial activity arises. Here, however, the divisions proceed no further. It will also be noticed that the intercellular spaces in the cortex are large. *Acorus* is a swamp-growing plant, and the tissues of water-plants are characterised by large intercellular spaces.

The arrangement of the vascular tissues thus seen in roots, with the xylem and phloem alternating on different radii, is described as

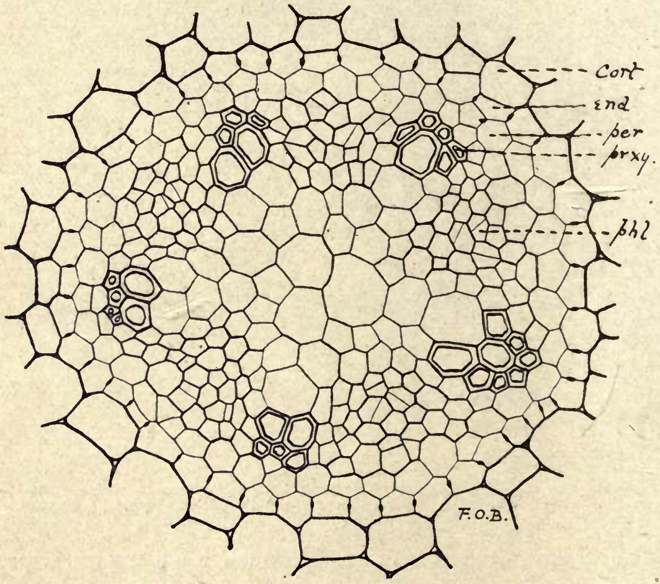


FIG. 56.
Transverse section of the stele of a young root of *Ranunculus*, showing the central metaxylem not yet developed. Lettering as before. (× 200.)

radial. It is in sharp contrast to the *collateral* arrangement characteristic of stems, where the xylem and phloem are upon the same radius, the phloem being outermost. Moreover, while in stems the protoxylem is directed centrally, in roots it is peripheral in position. Evidence of the centripetal succession of development can easily be seen in sections of young roots. Fig. 56 shows such a section from the Buttercup, which has five protoxylem groups, a number not uncommon for Dicotyledons. But of these only the protoxylem vessels are as yet developed; the vessels of the metaxylem are still thin-walled, but they extend to the centre of the pithless root, and they form a solid star of xylem when mature.

Since the arrangement of the vascular tissues is radial in the root, but collateral in the stem, it is obvious that a readjustment must take place where the one passes into the other. The change is effected in various ways in different plants, at or near to the level of the soil. The xylem-masses rotate upon their axes, and this is combined with splittings and fusions in some cases, so that the peripheral protoxylem of the root becomes central in the stem, and the xylem-masses range themselves internally to the phloem-masses. Thus without break of the continuity of the conducting tracts, the characteristic structure of the root passes upwards into that of the stem.

In order that the root may perform its function of absorption of water from the soil, a close relation with the soil must be established.

FIG. 57.

Representation of root-hairs in the soil. e=epidermis of a vertical root. h, h'= root-hairs grown out from its cells, and adjusting their growth to the solid fragments of the soil. Each of these fragments is covered by a film of water, which is shaded; while the clear spaces indicate the air-cavities in the porous soil. (After Sachs.)

This is the important duty of the root-hair. The parent cell that gives rise to it is usually oblong in form, and from a point about the middle or upper end of its outer face the hair arises as a cylindrical process, which penetrates between the particles of the soil. It adjusts its form to the spaces between them, while the nucleus passes out into the growing hair, and the delicate cell-wall is lined by a thin film of cytoplasm surrounding a central vacuole. A gummy softening of the wall near the distal end leads to a most intimate connection with any solid particle. The state of the root-hair in the soil is suggested by Fig. 57. As the water in the soil is held in the form of surface films

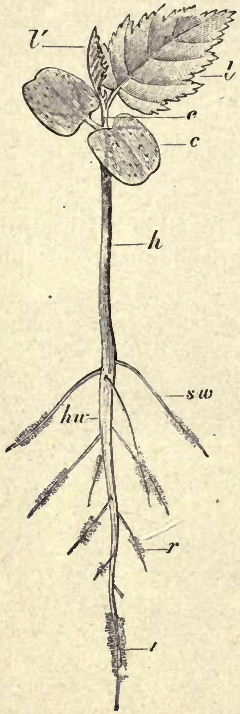


FIG. 58.
Seedling of *Carpinus Betulus*. *h*=hypocotyl. *c*=cotyledons. *hw*=main-root. *sw*=lateral roots. *r*=root-hairs. *e*=epicotyl. *l*=foliage leaf. Natural size. S.

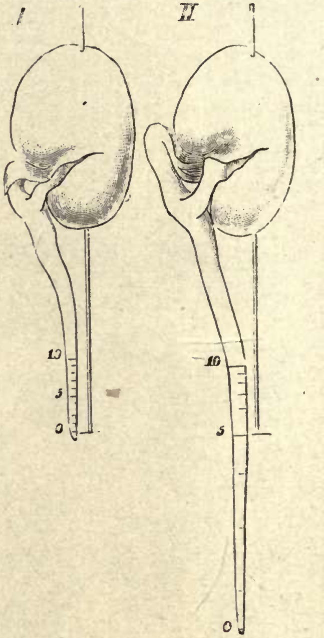


FIG. 59.
Localisation of growth near to the root-tip of *Vicia Faba*. In I. the root-tip has been marked with 10 zones 1 mm. apart. In II. the same root after 22 hours. The lines nearest the tip are now most separated owing to the growth having been there most active. (After Sachs.) S.

covering the several particles, the root can by its hairs tap those films, however thin they may be in a dry soil. It is important further to realise how numerous these root-hairs are. It has been estimated that over two hundred of them may be borne on one square millimetre of surface of the root of a Pea, while in other plants, for instance the Maize, the number may be still higher. The effect of this is greatly to increase the possible absorptive surface of the root.

The hairs arise in acropetal order. Individually they are functional only for a short time, as is seen from the fact that though active at a short distance backwards from the growing root-tip, at a further distance from the apex they may have already shrivelled away, so that the older part of the root no longer preserves its intimate relation to the soil. Thus as the root-system extends, it taps an ever larger area of the soil, while it is actively absorbent only at the outer limit of the area invaded (Fig. 58).

As soon as any part of the root is anchored in the soil by its outgrowing hairs, it could not possibly increase in length without tearing them away from their hold. But of this there is no sign. It follows, therefore, that the growth in length of the root must be restricted to the region beyond the youngest root-hairs. It may be demonstrated that the growth is thus restricted, and that the most rapid growth is close to the tip, by making marks with Indian ink at equal distances upon the outside of a growing root. The root should then be kept in condition as near as may be to the normal. After a period of twenty-four hours, if the distance between the marks be compared with the original scale, it will be seen that the two do not tally. It will easily be seen where the greatest elongation has been (Fig. 59). The most rapid growth in an average root is about 5 mm. from the tip. It diminishes gradually from that point in both directions, and ceases at about 10 mms. from the tip. This restriction of the growth in length to a short region behind the tip is characteristic of roots, and is in sharp contrast to what is seen in ordinary stems. In them the growth in length may be spread sometimes over a length of several decimetres.

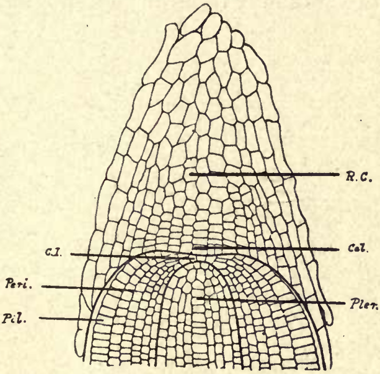


FIG. 60.
Root-tip of Barley, cut in median longitudinal section, and placed apex upwards. *R.C*=root-cap. *cal*=calyptrogen layer, which renews the tissue of the cap. *CI*=common initials for piliferous layer (*Pil*) and the periblem (*Peri*). *Pler*=central cylinder of plerome, giving rise to the stele (× 110.) (After Janczewski.)

A consequence of the growth of the region beyond the anchoring root-hairs is that the root-tip itself is forced forward. As in the stem, so in the root the apical tissue is embryonic, and of delicate texture. Nevertheless this delicate root-tip is driven through the soil, forcing aside the solid particles in its course. A study of its structure explains how injury to the apex is avoided. External observation shows that the conical apex itself is semi-transparent and slimy to the touch. By this sliminess it readily slides past obstacles, losing occasionally some superficial cells in the process. But the structure of the root-tip as shown in section explains the protection better; it is well shown for the common Barley in Fig. 60. The actual growing point is covered by a protective *root-cap*. The superficial piliferous layer as it approaches the apex, curves inwards, though still preserving its identity. Outside it lies a cap of tissue (*R.C.*), which though thick at the actual tip, gradually thins off as it spreads backwards. Its superficial cells are

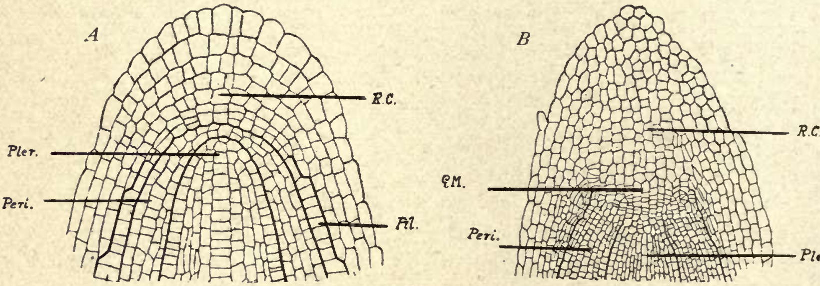


FIG. 61.

A=Root-tip of Buckwheat (×120.) *B*=root-tip of Pea (×60.) *R.C*=root-cap. *Pil*=piliferous layer. *Peri*=periblem. *Pler*=plerome. *GM*=the general meristem in the Pea from which the different tissues are gradually derived. (After Janczewski.)

only loosely attached. Their walls, being gummy and swollen with the water in the soil, are easily rubbed away. But the loss is made good by growth and cell-division arising from the innermost cells just outside the incurved piliferous layer. Internally the central stele continues up to the apex, ending in a rounded dome. At that point a single layer of cells intervenes between it and the root-cap. This layer gives rise by successive divisions to the piliferous layer and the cortex. There are thus in this type, which is common for Monocotyledons, *three definite strata* at the apex of the root, and each gives rise to a tissue which takes special characters as it matures.

The stratification of the growing point of roots is not always on the plan described, though that is the usual type in Monocotyledons. In Dicotyledons various conditions are seen, of which two examples may be given. The most common is that seen in the Sunflower and Buckwheat (Fig. 61, *A*), where the stele is as before a distinct column ending in a definite dome. The cortex is also a distinct tissue covering it, but reduced to a single layer at the extreme tip. The piliferous layer has a joint origin with the root-cap, by periclinal divisions of cells just outside the tip of the cortex. The chief difference is that the piliferous layer is distinct in origin from the cortex, while in the Barley they were seen to have a common origin. A second type is illustrated by the Pea and other Leguminosae. (Fig. 61, *B.*) Here the stele, cortex, piliferous layer, and root-cap all originate from a common mass of meristem, which occupies the apex, and segregates gradually into the several tissues as the cells mature. Such facts show that no theory of "germinal layers" can have any general application in the development of the plant-body.

The normal increase in number of roots is by the formation of lateral rootlets, which originate from deeply-seated tissues, and force their way

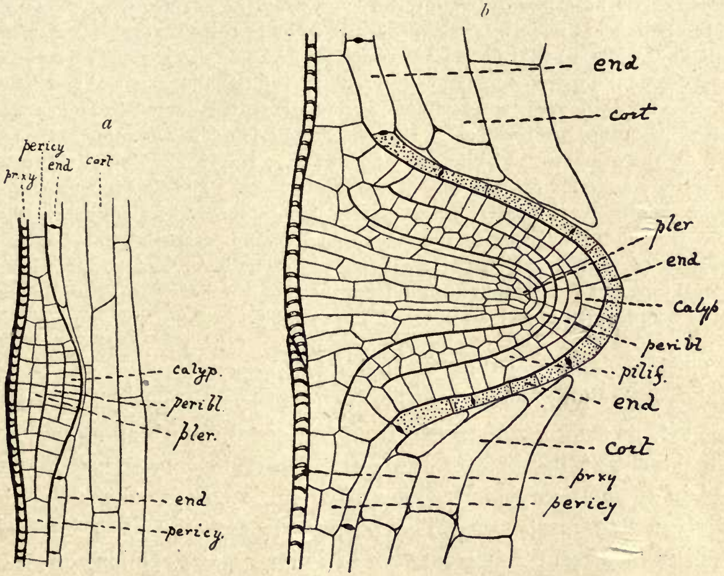


FIG. 62.

Origin of a lateral root from the pericycle, as seen in longitudinal section of *Reseda*. In (*a*) the pericycle has divided by periclinal walls to form four layers to which the tissues named are referable; the endodermis has yielded. In (*b*) the formative tissues are clearly recognised. The endodermis (*end*) has developed as a digestive sac. (× 100.) (After Van Tieghem.)

out of the parent root. Such an origin is described as *endogenous*, and is in contrast to the *exogenous* origin of leaves, where the surface-tissue remains continuous over the new growth. The lateral root springs from the cells of the pericycle, usually at a point opposite to one of the protoxylem-groups. If the parent root be cut longitudinally through the point where a lateral rootlet is being formed, the cells of the pericycle opposite the protoxylem will be found in active division (Fig. 62, *a*). Later the tissues thus formed give rise to the central stele (*pler.*), the cortex (*cort.*), piliferous layer (*pilif.*), and root-cap (*calyp.*), of the lateral root (Fig. 62, *b*). By reason of its deep-seated origin the tissues of the lateral root are intimately connected with the tissues of the main root. At its tip it pierces the cortex of the parent root by a process of digestion, through the activity of cells of the endodermis (*end.*), though in some cases cells of the cortex also take a part. They form a glandular *digestive sac* which softens the cells outside, so that they yield to the growing rootlet within. As their substances are absorbed, the rootlet may be said to eat its way out from the parent.

The details of division of cells in the formation of a rootlet vary in different cases. It is here illustrated for the type usual in Dicotyledons. The cells of the pericycle divide by periclinal walls, so as to form several layers, and by anticlinal walls, so that each layer consists of numerous cells. The innermost layer forms the plerome of the young root, giving rise to its central stele (*pler.*). The next outer layer is the periblem, giving rise to the cortex (*peribl.*); while the third outermost layer gives rise on the one hand to the root-cap (*calyp.*), and on the other to the piliferous layer (*pilif.*); the two having a joint origin, as already explained in the case of the Buckwheat. The consequences of this mode of origin are that the vascular tissues of the rootlet connect directly with the vascular tissues of the main root. This is essential to the effective transfer of materials. But the cortex, piliferous layer, and root-cap of the lateral root are all distinct in origin from those of the parent. Physiologically this discontinuity is not a matter of importance.

The individual root thus growing indefinitely at its apex, and bearing an increasing number of lateral roots, is subject to increasing demands upon it, as a means of transit from the distal absorbing region to its attachment at the base of the plant. In Monocotyledons (Fig. 55), and in some Dicotyledons (Fig. 56) there is no special development of tissues to meet this. The purpose is served by an increasing number of adventitious roots, as in Palms, Maize, Onion, etc. But in most Dicotyledons, and especially in those that are woody, there is a process of *secondary thickening by means of a cambium*, analogous to that seen in their stems. Cell-divisions appear in the conjunctive parenchyma lying internally to the several groups of phloem (Fig. 63, *a*). Arcs of cambial activity are thus formed, which soon spread to the tissue of the pericycle lying peripherally to the protoxylem (Fig. 63, *b*). The several arcs are thus linked together to a continuous band, in form of a corrugated cylinder. As in the stem, this cambium produces secondary wood internally, and secondary bast externally, to an indefinite degree. But at first the cells lying peripherally to the protoxylem form only parenchyma, so that a broad medullary ray appears externally to each group of the primary wood. In the secondary wood additional medullary rays and annual rings may

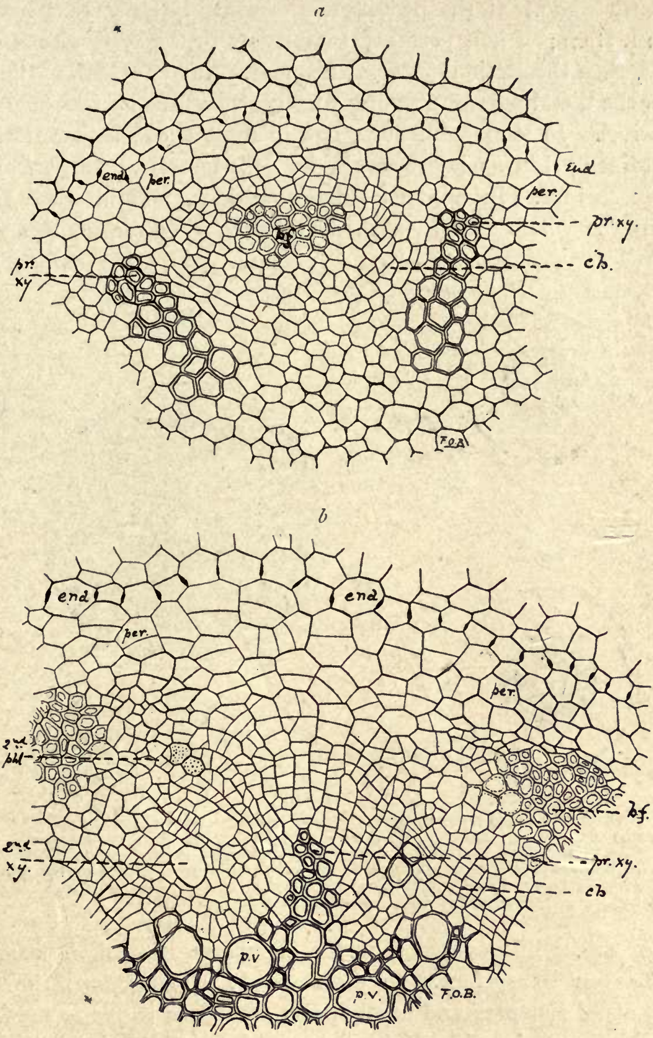


FIG. 63.

a, b, Successively older sections of the root of the Bean (*Vicia Faba*), showing the beginning of cambial activity. In (*a*) divisions appear (*cb*) in the conjunctive parenchyma internally to the phloem, but the pericycle (*per*) is quiescent. In (*b*) the cambium has already formed xylem internally (*2nd xy*), and phloem externally (*2nd phl*), and cell division has spread to the pericycle, and is continuous outside the protoxylem (*pr.xy*). (× 100.)

appear, as in the stem. Consequently an old root of a Dicotyledon acquires a structure very like that of an old stem (Fig. 64). The difference may be often observed even in old roots by looking for the primary wood. If the protoxylem is central the section has come from a stem; if it is peripheral relatively to the rest of the primary wood, then the section has come from the primary region of the root.

As the distal part of a young root grows older the root-hairs upon it shrivel. In Monocotyledons, and in some Dicotyledons the cortex is retained; but as it grows old its cells lose their turgor, and the cortex shrinks. In bulbous Monocotyledons, and in some Dicotyledons the whole root then shortens, anchoring the plant firmly in

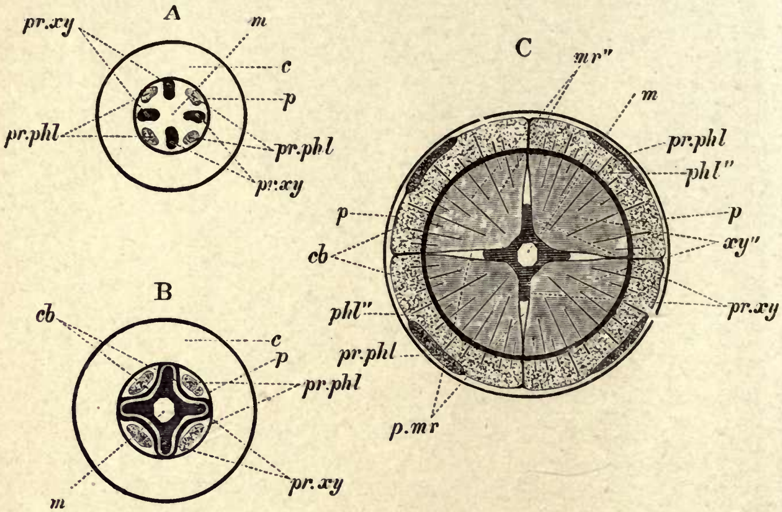


FIG. 64.

Diagram A shows arrangement of tissues in a young root of a Dicotyledon before cambial activity begins. B, the same when cambium can be clearly recognised. C, after secondary thickening has progressed. *c*=cortex, present in A and B, but in C it has been thrown off. *pr.phl*=primary phloem. *phl″*=secondary phloem. *pr.xy*=primary xylem. *xy″*=secondary xylem. *p.mr*=primary medullary ray. *mr″*=secondary medullary ray. *m*=pith. F. O. B.

the ground, while evidence of the shrinkage is seen in transverse wrinkles on its surface. In most woody Dicotyledons the bulky cortex itself collapses and finally peels off. This is due to the formation of a band of cork, which originates from the pericycle, and cuts off the outer-lying tissues from physiological connection with those within, so that they perish. Since the cortex makes up a very large proportion of the whole bulk of the root, the consequence in such cases is that at first the root appears to become thinner as it grows older. But as a matter of fact the central stele has meanwhile been increasing in bulk, and it is protected externally by the band of cork which originates from the pericycle. Since this cork may be further developed as in stems, the old root is covered by a band of bark not unlike that of a woody stem.

The stem, leaf, and root, as seen in ordinary Flowering Plants, have now been described. In subsequent chapters the Plant-Body can therefore be considered as a connected whole, and some idea gained of its physiological position as a concrete living organism. Normally, with its root in the soil and its shoot in the air, it acts as a sort of intermediary between the two regions in which it lives. One phase of the Botanical interest will be to see how the Plant plays off the one medium against the other, drawing meanwhile its nourishment from both. Another phase is to follow the materials abstracted and to see how they are used in Life, and how on the disorganisation of the Plant after Death that material is finally restored to its original source. Vegetation may thus be looked upon as an active factor in that interchange and circulation of material which is constantly taking place at the surface of the Earth's crust.

CHAPTER VI.

THE WATER-RELATION.

If you neglect to water plants grown in pots, the plants will wither; if the withering has not gone too far the plant may recover after watering; but if the neglect has been too prolonged the plant will die. These facts are familiar to everyone who has grown plants in pots; and though the problem of water-supply may perhaps be less obvious in plants growing naturally in the open, it is no less a grave one for them also.

In discussing the relation of plants to water it is necessary in the first place to realise how high is the proportion of water contained in ordinary plants. If a block of wood be cut out from the trunk of a living tree, and weighed, and after drying out thoroughly at 100° C., it be weighed again, it would be found to have lost about half its weight. Thus water forms about half of the weight of so solid a tissue as the wood in the normal living state. In succulent tissues of the leaves or young stems, or in the tissues of herbaceous plants, the proportion is much larger. In the case of the fresh Cabbage it amounts to about 89 p.c., and in the Lettuce, as cut fresh for a salad, to about 96 p.c. Thus only about 4 p.c. of a crisp Lettuce consists of the substance of protoplasm, and cell-walls. The living plant may then be regarded as a structural framework retaining within it a very high water-content. The water exists there in various forms. A large part of it appears as *liquid water*, filling the vacuoles of cells, or in the cavities of the vessels, and it can be seen as such microscopically. But a considerable proportion of it is absorbed into the substance of the protoplasts, or the cell-walls and starch-grains, as *water of imbibition*, upon which their swollen condition depends. Some may be present as "*water of constitution*," entering more intimately into relation with the substances of which the parts are composed.

The Shoot and Root together form this water-containing Plant-Body. Their constituent tissues are continuous from one to the other. This is especially to be recognised in the case of the vascular skeleton. It may be traced as extending without break from the apex of each root continuously to the main root, and onwards to the base of the stem, where its strands undergo a rearrangement in passing from root to stem, but no break of continuity. Thence the strands of the vascular system extend upwards to the leaf-bases, and out to their extreme tips and margins. Similarly with the axillary buds, or the branches developed from them: their vascular system is connected at the base with that of the main shoot. This continuous vascular skeleton is embedded in softer tissues, mostly parenchymatous, and with a relatively high water-content. The dermal tissue forms a complete superficial skin over the whole shoot. It covers the surface of stem and leaf, and is even extended downwards, though with modification of its characters, to the root. Since its cells form a continuous skin, and their outer walls are covered by an impervious film of cuticle, the shoot is thereby protected from indiscriminate loss by surface-evaporation of the water it contains in so large a quantity. But as the atmosphere in which the shoot is exposed is almost always below the point of saturation with water-vapour, such evaporation is liable constantly to occur, just as in clothes hung out to dry. It is checked, however, by the cuticular covering, except where this is interrupted by the pores of the stomata. These are present on the stem, but are specially numerous on the lower surface of the leaves. Thus the superficial skin is porous. The stomata are not always open; they act automatically, opening and closing according to external conditions. Thus they serve as an adjustable control upon the loss by evaporation, or, as it is termed, *Transpiration.* The loss is made up in the normal plant by absorption of water from the soil by the roots. It is then transmitted upwards along the vascular tracts. Thus a stream of water passes through the plant, varying in volume according to the conditions. This is called the *Transpiration-Stream.*

The Transpiration Stream

The root-system from which this stream originates is buried in the soil, which is a mass of mixed materials, organic and inorganic, holding within it water in greater or less degree. No soil in the open is ever actually dry. Normally the amount of water it contains is considerable. It is partly held as water of imbibition in the *Humus.* Partly it consists of a film of water, of varying thickness according to the amount of water present, which covers each solid particle of which the soil is composed. An important point is that the water forming these films is mobile. It can move from place to place, equalising the thickness of the films throughout, so that if water be drawn off at any point in the soil it can be made good by the flow of compensating water towards that point. Consequently any rootlet closely related to the particles of the soil has at its disposal, within certain limits, the whole reservoir of water which the soil in its near neighbourhood contains. (See Fig. 57.)

The root-hairs partially enwrap the particles of soil with their gummy walls, and so gain access to the film of water covering them. Each hair is a vacuolated cell, with a film of living cytoplasm intervening between the vacuole-fluid within and the covering cell-wall. The latter is a permeable membrane, through which water and substances in solution in it can pass by filtration ; and it has access to the water in the soil, and is saturated by it. But the *living cytoplasm* is a semi-permeable membrane (p. 25). During life it can control the passage of materials dissolved in its cell-sap, such as sugars. Thus, osmotically active substances are within the protoplasmic film, while outside is the soil-water with various other substances in solution in it. The living protoplasm acting as a controlling influence, there is a passage of water, and also of certain of the substances in solution in it, into the root-hair, while the living protoplasm exercises some degree of selection upon these. Thus, *under protoplasmic control*, *water and certain salts enter into the plant-body.*

The water thus absorbed from the soil is transferred by a "*slow*" movement from cell to cell. It passes, under the control of the protoplasts of the cells of the exodermis, into the cortex, which serves the young root as a temporary reservoir. Again, under control of the protoplasts of the endodermis, it passes into the stele, and there meets at near hand the conducting tissue of the xylem. Thence it may be transmitted by a "*quick*" movement throughout the conducting system of the plant. Finally, it may be distributed again through the agency of individual cells to the points where it is required.

At the beginning and at the end of the course thus traversed, the Transpiration-Stream passes cell by cell, and its movement is under protoplasmic control. But *in the conducting tract of the wood it passes through the cavities of the vessels and tracheides, and through the permeable pit-membranes.* This can be shown by means of coloured fluids, which readily traverse the wood of a living plant from a cut surface, following the cavities of the vessels, which they stain. Negative evidence of the fact may be gained by plugging the cavities of the vessels of a cut shoot with gelatin: the stream is then stopped, and the subject of the experiment withers, though an ample supply of water may be accessible at the cut surface. It may thus be concluded that it is through the cavities of the vessels or tracheides that the quick movement of the Transpiration-Stream passes. The mechanism of its movement is still obscure in some points, but it may be analysed so that for plants of moderate size it is intelligible. Two factors are recognised as effective, though these probably do not provide a complete explanation of the movement. *There is a motor influence from above, and another from below.* Either or both may be intermittent in their action. That from above is *suctorial*, that from below is *propellent*. That water is drawn into a cut stem may be demonstrated by Farmer's bottle (Fig. 65). It is closely fitted with a rubber bung traversed by a funnel and stop-cock for supply (*F*), and by a length of thermometer-tubing, bent as shown, with its end open (*r*). The apparatus thus forms a closed system, open to pressure of the air only at the end of the tube. The cut stem of a suitable shoot is passed through the bung; it must be closely fitted, and the whole apparatus completely filled with water up to the end of the tube. The end surface of the water column will then, under normal day conditions, be seen to move inwards along the tube. Since the apparatus is closed and full of fluid, the movement of the column backwards in the open tube shows that water has been absorbed at the cut end of the shoot. The length of the tube emptied in a given time will give a rough measure of the amount of

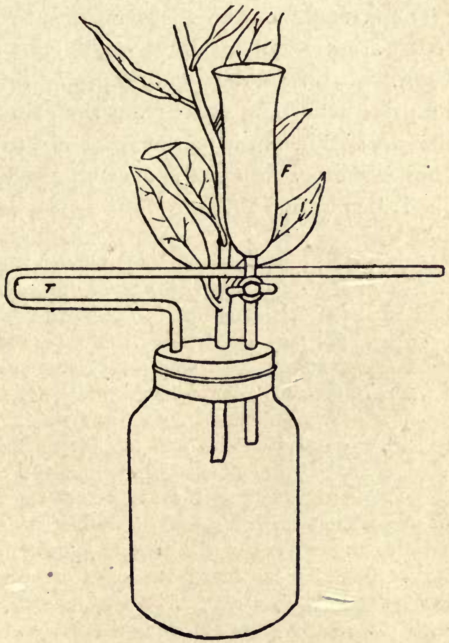


FIG. 65.
A simple Potometer, for indicating and measuring the amount of water absorbed by suction at the cut base of a shoot. (After Farmer.)

water thus absorbed. This apparatus may be used to show how the amount absorbed depends upon external conditions. Thus the shoot may be covered by a glass bell, which will have the effect of diminishing the amount; or it may be placed in a draught of air, which will increase it. Or observations may be made at different temperatures, and under different conditions of lighting, so as to test the effect of these also upon the amount taken in to make up for loss by transpiration.

The strength of the suctional influence may be demonstrated by fitting a cut shoot by an air-tight joint into a glass tube filled with water, with its lower end dipping into mercury. The suctional influence, absorbing water from the column in the tube, will raise the mercury to a height in some cases equal to a suction of one atmosphere. Thus *suction from above* is a very active factor in the movement of the Transpiration-Stream.

If suction from above be transmitted from the transpiring cells to the cavities of the tracheides and vessels, through which the supply is conveyed, this at once directs attention to the nature of their contents, and to the pressures to which they are exposed. The vessels and tracheides are full of fluid when young. It has been shown by Dixon and Joly that an unbroken column of water in a closed tube, with its walls wetted by it, has such cohesion that it can transmit a tension like a rigid solid. By such unbroken columns of fluid in the young vessels and tracheides the suctional influence could then be transmitted from above throughout the conducting tract. Moreover, it has long been known that the contents of the vessels are normally at less than the atmospheric pressure, and an indication of this is seen by the absorption of water at the surface of a freshly cut stem. These facts support the conclusion that the suctional tension from above is transmitted downwards through the tracheae.

But as vessels grow old, bubbles of gas may frequently be seen in their contents, which would appear to break the fluid columns. The individual vessels are, however, continuous as open tubes only for a short distance, and tracheides are even shorter. Each is finally closed by a water-saturated wall, which is impervious to gas-bubbles. Hence these bubbles of gas would only expand, under reduced pressure, till they completely fill the tracheae in which they occur. The water-column of the stem would only be completely interrupted if the tracheae containing bubbles were to form in some place an unbroken diaphragm across the conducting tissues of the stem. Provided a few were still full of fluid, that would suffice for the transmission of the suctional tension downwards.

A difficulty may be expected to arise in the case of tall trees. But Dixon sums up the case for them thus: "The transpiring cells of the mesophyll normally remain turgid during transpiration; accordingly we would expect that in high trees the osmotic pressure keeping them distended must correspond in magnitude to the tensions necessary to raise the sap. This surmise has been confirmed by determinations of the osmotic pressures in the saps of various leaves. These pressures have always been found adequate to resist the transpiration-tension."

On the other hand there is also a *propellent* factor which may act *from below*. If a rooted stem be cut a few inches above the soil on a warm day, and the cut surface be immediately examined with a lens, it will appear dry. A drop of water placed upon it will at first be absorbed. But in a short time it will be found that water exudes from the lower cut surface, coming out from the cavities of the vessels. If a tube be fitted upon it with a tight joint, the fluid exuded will collect and rise in it. In the case of a potted Fuchsia plant about three feet high it has been seen to rise in a few days to a height of as much as 20 feet. Or a tube may be fitted as in Fig. 66, by which the pressure from below may be measured in inches of a column of mercury forced up by it. This demonstrates *Root-Pressure*, a second factor which may influence the movement of the Transpiration-Stream. These two factors can act simultaneously, though both vary independently. In the daytime normally the suctional influence is the greater, and this explains the fact that when first cut the surface of the stump appears dry, and water exudes only after some time has elapsed. The continuous movement of the Transpiration-Stream is chiefly due to these two factors, though it is possible that others participate with them in the case of tall trees.

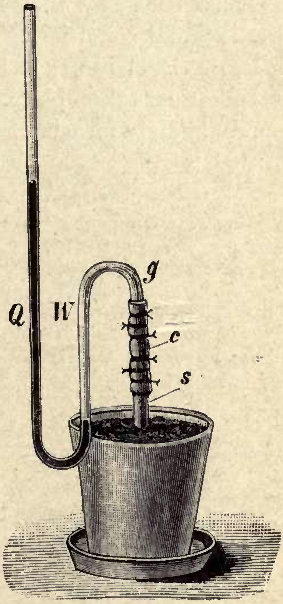


FIG. 66.
Arrangement for demonstrating root-pressure. The tube *g* is fitted on the cut stem *s*. Water is absorbed by the roots and forced into the tube, and the pressure can be measured in terms of the height of a mercury column (*Q*), which it is able to raise. S.

The water of the Transpiration-Stream is not pure water. This may readily be shown by evaporating some of the water extruded upon a clean glass surface, when a residuum will be left. It is composed of certain salts, together with sugar, and other substances. The most important contents as regards the general nutrition of the plant are the dissolved salts, though organic substances may also be present in solution. A prominent example is Maple-sugar in the sap of the Maple in spring. When the Transpiration-Stream moves up the plant in the form of fluid water through the vessels, the dissolved substances are conveyed upwards with it, and the stream is thus a means of transit. This is in fact the real importance of the Transpiration-Stream.

Control by the Stomata.

It has been seen that Transpiration varies in amount according to the external conditions. Those which promote evaporation tend to increase the stream. It is through the pores of the stomata that the evaporation takes place. The loss which actually occurs can be approximately measured by counterpoising on a balance a pot-plant, with its pot completely covered by a rubber bag closed round the stalk. Accurate weighings taken at intervals will show that the whole plant together with its pot loses in weight. The loss is approximately due to Transpiration. Taking the average loss per hour it is found to be less by night than by day. This may be partly explained by the average temperature being lower at night. But a more important factor is the *control by the stomata* themselves, which are automatic mechanisms that work in the following way. The guard-cells contain chlorophyll, which is usually absent from the ordinary epidermal cells. This produces under the incidence of sunlight an increase of osmotically active substances such as sugars. As the turgor of the guard-cells increases their curvature increases, and the pore opens. In darkness, however, the osmotic substances are gradually removed, and their turgor decreases. The guard-cells then straighten themselves, and the pore closes (Fig. 67, *A*, *B*). That their action depends upon the turgor of the cells is readily shown by treating an open stoma with a 5 p.c. solution of common salt; this relieves the turgor, and the stoma may be seen to close, with ultimate plasmolysis of its cells. The stomata are thus self-regulating organs, usually open by day and closed by night. Their behaviour goes far to account for the greater average transpiration of the plant by day

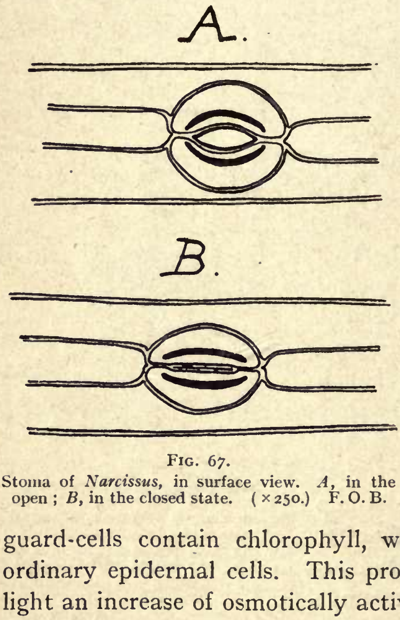


Fig. 67.
Stoma of *Narcissus*, in surface view. *A*, in the open; *B*, in the closed state. (×250.) F. O. B.

than by night. This explains how under day conditions the suctorial factor is chiefly effective in moving the Transpiration-Stream upwards.

The stoma is such an important organ in the life of aerial plants that its action deserves special attention. There is a good deal of variety of detail of structure in different cases, but the chief features are these. The two guard-cells, attached at their ends, are usually curved, the wall facing the pore being shorter than that in contact with the adjoining cells. The inner and outer slopes of the face next the pore bear each a projecting ridge. The

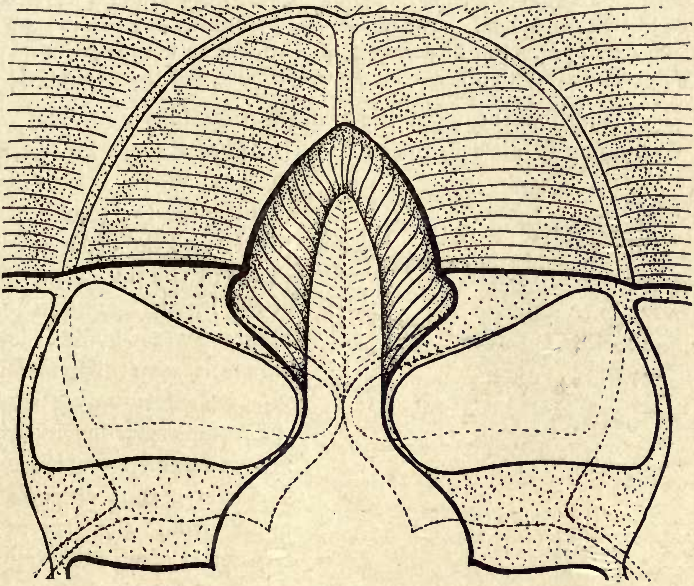


FIG. 68.

Diagram representing a stoma in median section, and also in surface-view. The continuous lines show the position of its guard cells in the open state, of turgor; the dotted lines show their position in the closed state.

action depends upon increase and decrease of the turgor of the guard-cells, as compared with that of their neighbours. The open stoma, with its tense cells, requires more room than the closed stoma. That room has to be gained by forcing the adjoining cells aside. Where the cell-walls are thick, special thin areas of cell-wall are found which are effective as joints or hinges, allowing the cells to adjust themselves mutually when the pore opens. Chlorophyll is present regularly in the guard-cells, while it is deficient or absent in most plants from the rest of the epidermis. Thus the guard-cells on the incidence of light increase their supply of osmotic substance more than these, and so increase their turgor. It is this increase of turgor, beyond that of the surrounding cells, acting on cells of the form and structure of the guard-cells, that makes the pore open (Fig. 68). The internal pressure being equal over the whole internal surface, since the convex wall presents a larger area, it will stretch more than the concave wall; and this would in itself produce a greater curvature, even if the walls were all of the same thickness. But they are not. The ridges of thickened cell-wall on the outer and inner faces of each guard-cell make the average thickness of the wall greater on the side next the pore. This will accentuate the curvature of the cells whenever their osmotic turgor rises. A further effect of the turgor will be to make the section of the cell-cavity approach as nearly as possible to the circular. This will result in withdrawing the projecting surfaces where the cells meet when closed. All these factors act together in opening the stoma. The increase of turgor is secured by the action of the chlorophyll whenever the guard-cells are exposed to sufficiently intense light. The consequence is that in daytime the stomata are habitually open. But in darkness, since the osmotic substances may be quickly drafted away to other cells, the turgor falls, and the stoma closes.

Under conditions of night the transpiration falls off. The roots still continuing to absorb, their action becomes the more prominent factor. Water may thus at night gorge the tissues of the plant, and is often seen to exude at the tips and margins of the leaves. Here in many plants water-glands exist, which by secreting water provide as safety-valves against the risk of water-logging of the intercellular spaces (Fig. 69). The water thus extruded at night from the leaves of Grasses is often mistaken for dew. A somewhat similar condition is seen in spring in woody trees before the leaves are fully developed. At this time if the stems be cut, water will exude in considerable quantity, a phenomenon known as "bleeding." These are consequences of the continued activity of Root when transpiration is not active.

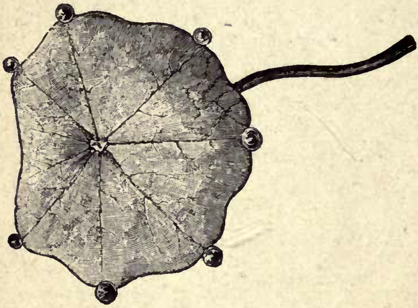


Fig. 69.
Exudation of water from the margin of the leaf of *Tropaeolum*, through water-stomata which are permanently open. (After Strasburger.)

The Transpiration-Stream providing the means of transit of salts in solution, and the water evaporating away, these salts will be concentrated at the place where the evaporation is active: that is, in the cells of the mesophyll of the leaf. Their cell-walls saturated with water abut directly upon the intercellular spaces. The water-vapour given off from them passes out, under control, through the pores of the stoma. Now the cells of the mesophyll are those which are most active in Photo-synthesis, for which certain of the salts are required.

It thus appears that those salts are landed by the Transpiration-Stream at the very place where they will be chiefly used, and in the daytime, when, as we shall see later, the constructive process is most active. Thus the Transpiration-Stream is not a mere method of making up what the plant has lost. It is actually the means of providing certain of those substances which are essential for the constructive nutrition of the Plant.

Food of Plants.

The next question will naturally be what substances they are which are transferred? The soil-water contains the substances in solution in it in a very dilute form. It would therefore be difficult to arrive by direct test at any conclusion as to the actual substances absorbed by the root. They can best be recognised by an indirect method, viz. by analysis of the plant-body, so as to show the actual substances of which it is composed. The elements involved may be grouped according to their constancy of occurrence, thus:

Constantly present: Carbon, Hydrogen, Oxygen, Nitrogen, Sulphur, Phosphorus, Potassium, Calcium, Magnesiun, and Iron. *Usually present:* Sodium, Silicon, Chlorine. *Occasionally present:* Manganese, Aluminium, Copper, Zinc, Cobalt, Nickel, Strontium. *Present in Seaweeds:* Iodine, Bromine.

It will be unnecessary to follow the occasional elements further. The chief physiological interest lies in those which are constant, for in them there is a probability of special physiological use. To obtain information on this point experiments have been made by *water-culture* (Fig. 70), the roots being grown in water in which the food-substances are dissolved. A full culture solution giving all the substances which are constant in the plant, excepting Carbon, may be made up according to various recipes. That of Sachs is as follows:

Water - - - - -	1000 cc.m.
Potassium nitrate - - -	1.0 gramme.
Sodium chloride - - -	0.5 ,,
Calcium sulphate - - -	0.5 ,,
Magnesium sulphate - - -	0.5 ,,
Calcium phosphate - - -	0.5 ,,
Ferric chloride - - - -	a trace.

The common calcium phosphate should be finely pulverised, and as it is only sparingly soluble it forms a sediment during the experiments. This recipe contains all the constant elements excepting Carbon. It also contains Sodium and Chlorine, but not Silicon. Such a solution supplied under certain precautions in a glass jar to the roots of a seedling may suffice for its full growth, and even for its flowering and fruiting. But the experiment may be varied by the omission of any one of those elements. Any constant change in the condition of the plant following that omission may be held as evidence of the part that substance plays in its normal physiology. This is most readily exemplified in the case of *Iron*. If the solution be made up with chemically pure materials, the result of growing it without Iron is that after the first leaves, which may appear pale green, the later leaves develop yellowish. If carried far the subject of the experiment will appear starved. If after this pale yellowish, or *chlorotic* state is well established a trace of Iron Salt be added to the solution, the normal green colour will be developed, appearing first along the veins; or even if it be applied locally to the surface of the leaves, the full green colour will appear at those points where the Iron Salt has been applied. The conclusion is that Iron is essential for the formation of the green colour, and that a very small quantity of it suffices. Similar experiments may be made by omitting other elements from the recipe, for instance Potassium (Fig. 70). Such results serve to show how important the Transpiration-Stream is in supplying the necessary salts from the soil.

FIG. 70.

Water-culture of Buckwheat. I. shows a culture where a full nutrient solution was supplied. II. shows the result of the omission of potassium. (From Strasburger, after Nobbe.)

WATER-ECONOMY.

The maintenance of the Transpiration-Stream is also important for the preservation of mechanical rigidity in the succulent parts. The flaccid and limp condition of the withering shoot, and the recovery which it shows on sufficient water-supply, are matters of common knowledge. Both are referable to the turgor of the individual cells, which falls when water is deficient, and the firmness of the whole tissue falls or recovers with it. Their turgor is also a necessary condition for Growth to take place; for it follows on the yielding of the resistant cell-wall before the internal tension, a permanent increase in size of the cell being the result. Thus adequate water-supply is essential for active vitality. But obviously a deficiency in moderate degree does not put a term on life, as the recovery of the wilted shoot shows.

In the case of any average Land-Plant, growing under average conditions, it is rarely that the water-relation presents any extreme

FIG. 71.
Succulent stem and flowers of a Cactus. (After Figuier.)

difficulty. A supply meeting the demand is usually available, and even herbaceous plants remain firm and do not wither beyond recovery under apparent drought and wind. But in plants which live in dry climates, or in positions where the water supply is apt to be deficient—such as sand, or on rock-faces where little or no soil is present; or in the case of plants which grow perched upon the branches of others (epiphytes), and thus have no direct access to the soil—the little water that is available must be used economically. If withering or actual drying up is to be avoided, special protection against undue loss by evaporation must be organised. This is done in various ways. The most direct is by reduction in the proportion of surface to bulk by assuming a rounded form of the stem with reduced leaves as in *Cactus* (Fig. 71); or of the leaves themselves, as in Stonecrop. In such plants the cuticle is found to be very well developed, while a waxy coating over the surface makes it a still better protection. The stomata are usually sunk in pits below the surface, while additional protection may be given by hairy or scaly coverings. (Compare Figs. 49, 50.) On the other hand, in certain plants exposed to sudden strong insolation, undue loss is prevented by permanent curling of the leaf with the stomatal surface within the hollow space, as in the Heath Family; or the curling of the leaf may be controlled by an automatic mechanism, giving protection in dry air, but opening out flat when the air is moist, as in many Grasses (see below, p. 156, Fig. 115). Plants thus modified in relation to drought commonly have a hard stiff texture of the shoot, often with spiny developments. To such plants the term *Xerophyte* is applied.

Such adaptive changes as these profoundly affect the general habit of individual plants; and the whole vegetation of a district may be characterised by them, giving a prevalence of hard and spiny bush, or of succulent herbage. There is no circumstance of life which impresses itself so deeply on the conformation of the plant as the water-relation. If, as we have reason to believe, vegetation was originally aquatic, in which condition there is no pressing water-problem, the spread of plants to the land opened new risks and physiological difficulties, while it presented, on the other hand, very positive advantages. The various adaptations which plants show in meeting the danger of undue loss by transpiration present to the mind the results of a struggle against circumstances, which could only be met by such means. But still it should be kept clearly in view that transpiration in moderate degree is essential to the well-being of land-living plants; for it is the means of leading the food-supplies from the soil in solution to the required spot.

It is in solution that all of these supplies come. There is in the normal plant no ingestion of food in mass, followed by gradual digestion. All food is acquired by the plant molecule by molecule. This is in contrast to animal nutrition. The *Amoeba* envelops solid particles of food in its naked protoplast, absorbs from them what it can, and ejects what it cannot digest. But in the plant the vegetative protoplasts are habitually encysted by a cell-wall, so that ingestion of solid particles is impossible. It follows directly from their encysted structure that the nutrition of plants must be solely by substances in solution. The ultimate importance for plants of the water-relation lies then in nutrition. For water is the medium of presentation of the soluble nutriment, which can thus pass through the cell-wall to the active protoplast within. It is in the protoplasts that the plant is able to build up its own organic compounds, using for that purpose the substances thus acquired.

CHAPTER VII.

NUTRITION, STORAGE, AND RESPIRATION.

THE Green Plant, supplied as we have seen with soluble salts from the soil, is able under certain conditions to construct new organic materials by a process carried on in its green parts. Such a process may be included under the general term *Constructive Metabolism.* But it is better to style it more specifically *Photo-Synthesis*, because it is a constructive process for which exposure to light is a necessary condition. It was formerly called Assimilation; but this term is unsatisfactory, for it has been used in Animal Physiology to connote the absorption of organic material already formed, whereas *in Photo-Synthesis new organic material is elaborated by the plant itself.*

The conditions necessary for Photo-Synthesis to proceed are these:

(1) *Chlorophyll* must be present in the cells which carry on the process.
(2) *Carbon dioxide* must be accessible to them.
(3) They must be exposed to *light* of sufficient intensity.
(4) The *temperature* must be within certain limits.
(5) There must be a supply of certain *mineral salts.*

The green colouring matter *Chlorophyll* is located in the chloroplasts. These may be found in the tissues of the stem, or even occasionally in roots, but only in parts exposed to the light. The leaf is their chief centre, and in the mesophyll particularly (Figs. 71 A, 72). Wherever chloroplasts exist they may act in Photo-Synthesis, for which their presence is necessary. The green colouring matter which they contain is soluble in alcohol, and may thus be extracted, leaving the discoid chloroplasts colourless. The green leaf itself, or the solution of chlorophyll in alcohol, if examined spectroscopically will show certain absorption bands, of which the most noteworthy are two well-marked bands close together in the red, and three broader bands, which in strong solutions obliterate the greater part of the violet end of the spectrum. From this we learn that by chlorophyll, which is necessary for Photo-Synthesis, certain red and violet rays of light are actually stopped and absorbed. It is also known that light which has passed through green leaves is less effective in Photo-Synthesis than an equal intensity of normal light. *These facts indicate that the absorbed rays are intimately connected with the synthetic process.*

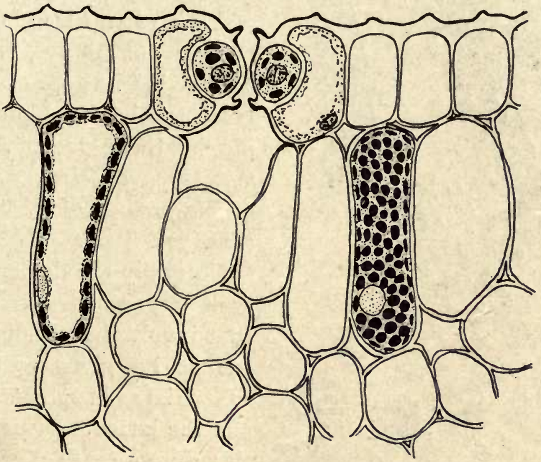


FIG. 71A.
Part of leaf of *Narcissus* in transverse section. Two of the cells of the mesophyll are drawn in in detail: that to the right as seen in surface view from without; that to the left in optical section. The chloroplasts are shown black. (× 300.) F. O. B.

Carbon dioxide is present in atmospheric air constantly, but in very small proportion. The latest estimates rate it normally at about 3 parts in 10,000. But as its molecules are mobile among those of the other atmospheric gases, it follows that if molecules of the gas be absorbed at any point, the place of those absorbed will be immediately taken by others from a distance. Thus the small proportion in which carbon dioxide is present is no disadvantage. The case of submerged green plants is much the same as that of sub-aerial plants. Their supply of carbon dioxide is presented in solution in the water which bathes their surfaces. Here again the supply is mobile and subject to diffusion in the water. Thus, whether in the atmosphere or in solution in water, even where the proportion of CO_2 is small, it is readily available for the purposes of the plant.

Under the normal day-conditions of a temperate climate the *light* and *temperature* fall within the limits of intensity necessary for Photo-Synthesis to proceed, while the Transpiration-Stream supplies the *salts* required, including those of Potassium and Iron. These necessary conditions being met, *the constructive process consists in the absorption of carbon dioxide, fixation of the carbon, release of free oxygen, and the appearance in the active cells of material formed from the carbon which has been fixed.* Commonly, though not always, it is starch that makes its appearance, and it is located in the chlorophyll corpuscles themselves. *Starch may then be recognised as the first visible product of Photo-Synthesis* (Fig. 72).

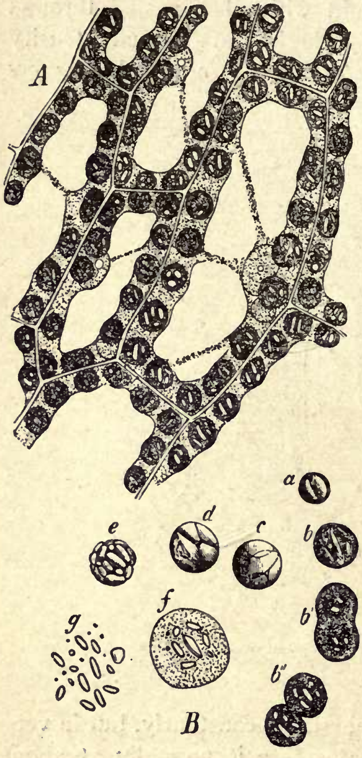


FIG. 72.

A. Chlorophyll granules in cells of the leaf of *Funaria*, showing small starch-grains included in them. *B* shows stages of division of the chloro phyll granules. *f* shows the included starch-grains after the granule has swollen in water. (After Sachs.)

Naturally the demonstration of such a gaseous interchange as that involved in Photo-Synthesis cannot be given so readily in sub-aerial as in submerged plants, and the latter are usually used for this purpose. If a single shoot of the common Canadian Water Weed (*Elodea*) be fixed below the level of water in a glass jar, with the cut end of the stem pointing upwards, and the whole be exposed to the light, bubbles of gas will be seen to be extruded in succession from the cut surface, and to rise through the water (Fig. 73). These are bubbles of *oxygen.* Arrangements can easily be made to collect the gas in bulk from a mass of specimens, and to subject it to the usual tests. *These bubbles of oxygen are a visible bye-product of Photo-Synthesis, and they may be used as a measure of the activity of the process.* The bubbles are approximately of equal size, and the number of them liberated in a given time may be counted. In this way it may be shown that the activity is greater in direct sunlight than in diffused light: that red, orange, and yellow rays of the spectrum are more effective than those of the blue or violet; and that the process itself depends upon the presence of carbon dioxide dissolved in the water. Thus, if water be used from which the carbon dioxide has been driven off by boiling, the bubbles of oxygen will not be discharged.

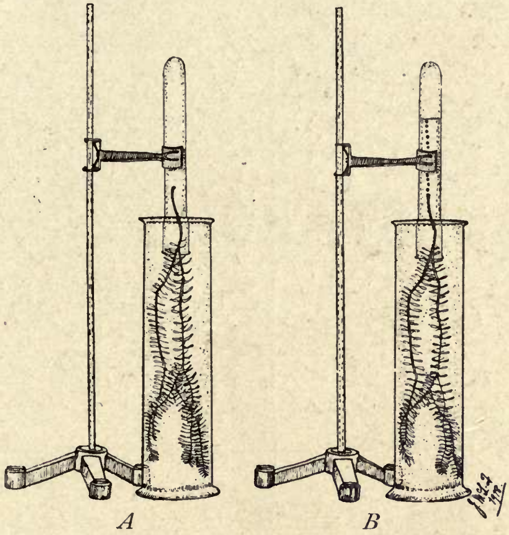


FIG. 73.

Arrangement for showing oxygen given off in Photo-Synthesis. *A*, before exposure to light, the tube is filled with water. *B*, after exposure for some time. A large volume of discharged gas has collected in the tube.

The relation of the activity of Photo-Synthesis to temperature has been illustrated by observations on the leaves of *Hottonia*, as reckoned in the number of gas-bubbles given off in five minutes, during which period the temperature remained constant. At 14° C. the number was about 200. When the temperature was raised to 31° C. the optimum number of about 550 was reached, while at 56.5° C. the activity ceased.

The effect of light in Photo-Synthesis is strictly local, that is, it is limited to those points where the rays actually fall. This is shown by experiments with stencil plates. Letters or other figures are cut out of an opaque card or tinfoil; or a plain strip will serve. It is applied closely to the surface of a green leaf of a living plant, which has previously been kept in the dark for two days, so that the starch will have been completely removed from the cells (see p. 111). The leaf should then be exposed to sunlight for six hours or so. If it then be removed, boiled for a minute in water, decolourised with alcohol, and stained with

Iodine solution, the exposed areas will take a dark purple stain, indicating the presence of starch, while the shaded parts will be yellow (Fig. 74). Microscopic examination of the mesophyll of the exposed parts will show that small starch-grains are included in the chlorophyll-corpuscles, while those of the shaded parts contain none. Thus *starch*

Fig. 74.
Results of experiment to show that the effect of light in Photo-Synthesis is strictly local. See Text.

appears only where the light falls, and it appears actually in the chloroplasts, which are thus recognised as the active agents in the process.

An experiment indicating that the decomposition of carbon dioxide does take place at the expense of the rays absorbed by the chlorophyll has been arranged by Timiriazeff (Fig. 75). Into each of a series of glass tubes containing air and a certain percentage of carbon dioxide a green leaf (uniform in size, and from the same plant as the rest) was inserted, and the tubes exposed to the spectrum of the sun in a dark room, so that rays of different refrangibility played upon each (II). After a few hours, analysis of the gases in the several tubes was made, and the results compared. It was found that the rays which are not absorbed by the chlorophyll do not decompose carbon dioxide, whereas the rays which are absorbed do decompose it, and that the activity is in proportion to the completeness of their absorption. The results are shown for the rays of the red end of the spectrum by the curve in Fig. 75, III.

It may be shown that the volume of carbon dioxide absorbed is approximately equal to the volume of oxygen given off in Photo-Synthesis by the use of Hofmann's apparatus (Fig. 76). It consists of a tube shaped like a horse-shoe, with one side closed, the other

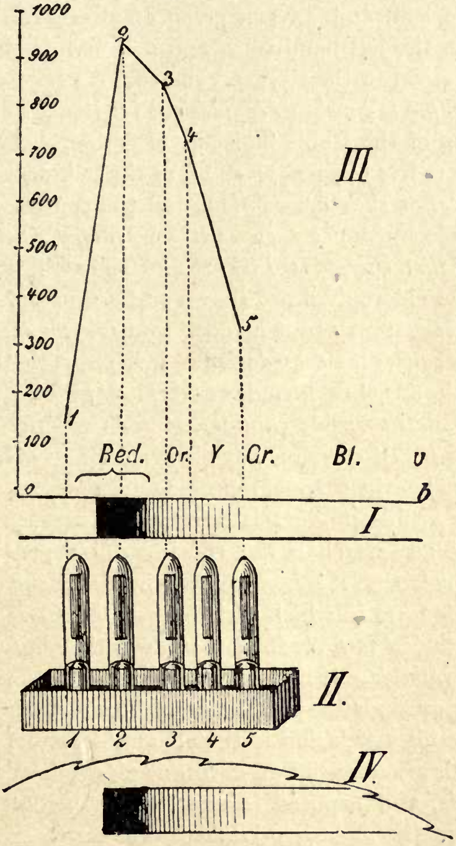


FIG. 75.
Arrangements for experiment of Timiriazeff to show that the decomposition of carbon-dioxide takes place at the expense of the rays absorbed. See Text. (After Timiriazeff.)

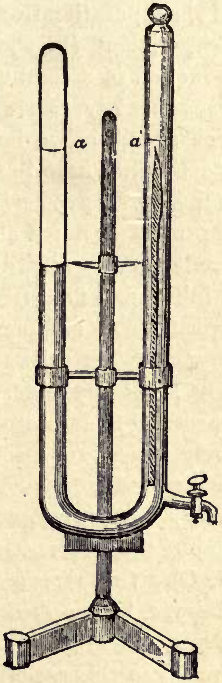


FIG. 76.
Hofmann's apparatus. (After Timiriazeff.) See Text.

fitted with a stopper. The whole tube is first filled with water. Carbon dioxide is then passed into the left-hand side of the curved tube which is closed, so as to fill it to a certain marked point. A green leaf is then passed into the right hand side of the tube, and its end is also closed; the whole apparatus is then exposed to sunlight. Gas will be evolved in the right limb, and the level of the fluid will fall, but at the same time the level will rise in the left-hand tube. It will be found that the gas evolved on the right is approximately equal in volume to that absorbed on the left. Tests show that the right-hand gas is oxygen, while the left-hand gas is still carbon dioxide. What has happened is that as the carbon dioxide in solution in the water is absorbed by the leaf, and oxygen given off, fresh carbon dioxide is withdrawn from the left-hand tube, and it is seen that its volume is approximately equal to the oxygen evolved.

The process of Photo-Synthesis involves deoxidation, for its first step consists in the breaking up of the stable molecule of carbon dioxide, and the separation from it of free oxygen, given off as the bubbles seen in experiment (Fig. 73). *For such deoxidation*, and the consequent production of a combustible substance such as starch, *energy must be expended. The source of that energy is Light*; and since the rays which are absorbed by the chlorophyll are shown to be those which are active in Photo-Synthesis, it may be concluded that it is *the energy of the absorbed rays which causes the deoxidation.* It is probable that the process is not a simple one, but includes several steps. In the interchange of gases, and in the visible product, starch, we only see the initial and final results. But starch is not always the first visible product. Oil globules make their appearance in some cases, *e.g.* Musaceae. In others no visible product is directly observed, as in many Monocotyledons. Since starch is not the invariable product first seen, it seems not unlikely that it is here, as elsewhere in the plant, merely a compact insoluble form in which carbohydrate is put aside. It is derived from sugar, and *it is probable that sugar is the substance actually formed in Photo-Synthesis.* It has further been suggested that a step in the constructive process is the production of formic aldehyde (CH_2O). One reason for this conclusion is that if an Alga, such as *Spirogyra*, be supplied with a weak solution of formic aldehyde in the absence of carbon dioxide, and exposed to the light, it will form starch. In this expeiiment the plant is presumed to be saved one of the constructive steps by receiving the formic aldehyde already formed. A further step might be the polymerisation of the formic aldehyde to form sugar, and so on to the starch which we see. These are, however, matters rather of theory than of demonstration, and it must be admitted that exact knowledge of the steps of the Photo-Synthetic process is still wanting. But none the less is it certain that the construction of new organic material is actually carried out.

It is well to form some concrete idea of the amount of material gained in the process. It has been calculated that the amount of starch formed by a square metre of Sunflower-leaf on a summer's day would be about 25 grammes. This quantity of starch should be weighed out in scales, it will then be seen to be a very considerable bulk. In forming these 25 grammes the plant would clear the carbon dioxide from about 50 cubic metres of atmospheric air, while for each gramme of starch formed about 250 to 400 cc. of water of the Transpiration-Stream would be evaporated. These approximate statements give some idea of the activity of the changes attending Photo-Synthesis on a summer's day. But it is not only this degree of activity that makes the constructive process in green plants notable. It must in a sense be recognised as the starting-point of all physiology. For to it the origin of all other organic substances may be referred.

It may not be strictly correct to say that all the combined carbon in the organic world was derived ultimately by Photo-Synthesis from the carbon dioxide in the atmosphere, though for practical purposes it is so. A small amount is obtained by nitrifying Bacteria, by action that is not dependent on light, or on the presence of chlorophyll. If these organisms, derived from garden soil, be grown in a culture solution containing potassium phosphate, magnesium phosphate, sodium or magnesium carbonate, and common salt, they will flourish. But the carbon they contain is obtained from the carbon dioxide of the air, not from the carbonate supplied. The nitrifying Bacteria thus have the power of forming a small amount of organic substances from the atmosphere, by a process altogether different from that of green plants.

Use of Carbohydrate to Form Proteid.

The carbohydrate acquired by the plant in Photo-Synthesis is removed by diffusion from the cells where it is formed. This may be readily proved if after active Photo-Synthesis and production of starch, the plant be kept in the dark for a few hours. The chloroplasts will then be found to have been completely cleared of the starch which they previously contained. A considerable proportion of this carbohydrate is probably used up directly in the *construction of proteid*, which is essential for the supply of the growing and dividing protoplasts. In addition to Carbon, Hydrogen, and Oxygen, all the proteids contain nitrogen (15-19 p.c.), and sulphur ($\frac{1}{2}$-$1\frac{1}{2}$ p.c.), and in some cases phosphorus also. Accordingly the construction of proteids requires a supply of these elements, and the source of that supply must be considered.

The question of the *supply of nitrogen* lies at the root of all plant-nutrition, for no protoplast can be formed without it. If in a culture-solution nitrogen be available in the form of nitrate, and all the other necessary supplies be present, the growth of the plant shows that its requirements are fully met. But if no combined nitrogen be given, the plant will show signs of starvation, and remain dwarfed. The conclusion is that though bathed by atmospheric air, of which the chief constituent is nitrogen, the plant cannot lay hold of the nitrogen in the free state, but *must be supplied with it in the combined form.* This is so for all ordinary green plants.

FIG. 77.
Root of *Vicia Faba,* with numerous root-tubercles. Reduced. (After Strasburger.)

But the case is different with some green plants, and especially with the Pea Family (Leguminosae). It has long been known to farmers that it is an advantage to have a crop of peas, beans, clover, vetches, or some such Leguminous plants in regular rotation with other crops in successive years. The roots of these plants are ploughed in after the surface crop has been taken, with the result that the soil appears to be enriched. Culture experiments on such plants have shown that they are able to obtain their nitrogen-supply from the atmosphere, and that this capacity is related to certain swellings (tubercles) present upon their roots. (Fig. 77.) These consist of tissues connected with the cortex of the root, and traversed by vascular strands. Their cells are densely protoplasmic, and are crowded with foreign organisms of bacterial nature (*Bacillus radicicola*). These gain access to the tissues of the young root through the root-hairs, and multiply rapidly in the tissue outside the stele. The invaded cells grow, and divide till a large tubercle is formed. When the roots bear these tubercles, it is found by culture experiments that the plant as a whole can increase its supply of combined nitrogen, and the only source of its supply must be the free nitrogen of the air. The way in which this is effected is by a mutualism between the Bacillus and the cells of the root. The latter supply the carbohydrate which the Bacillus requires. This like a few other bacteria, can use atmospheric nitrogen in the formation of proteids, and flourishes greatly. But finally a large proportion of the hypertrophied bacterial cells are digested, and their substance absorbed into the host plant. Thus the advantage to the Bacillus seems to be only temporary: that to the host-plant is a permanent addition to its store of nitrogen. (See Chap. XI.)

In addition to this source of combined nitrogen it seems probable from comparison of crops taken from plots of land without, and those with the addition of manure, that a considerable fixation of nitrogen takes place in the soil. On the other hand, certain nitrifying bacteria are known to oxidise ammonia into nitrous acid, and this further into nitric acid. By this means they obtain a supply of energy quite distinct from that derived in green plants by Photo-Synthesis and subsequent respiration. The practical result as regards the nitrogen-supply in the soil is that the products of decay in the form of ammonia-salts are converted into nitrites and nitrates, in which latter form combined nitrogen is most readily absorbed by the roots, and used by ordinary green plants. While the nitrifying bacteria thus gain their own physiological ends, they also play an important part in the circulation of nitrogen in organic life.

In some few plants a supply of combined nitrogen may be obtained by parasitism, or by the still more unusual carnivorous habit. But for the moment it must suffice to mention these. (See Chap. XI.) To sum up: *the majority of plants take up their nitrogen in the combined form from the soil, and do not use the free nitrogen of the atmosphere. But some few are able to do this, as in the case of the infected Leguminosae*; *while occasionally the supply in combined form is wholly or in part based upon a parasitic or a carnivorous habit.*

The supply of *sulphur* is from salts in the soil. Culture experiments show that *its supply in the form of sulphate is satisfactory.* It may well be that much of it passes into the plant in the form of calcium sulphate, while the calcium liberated when proteids are formed may be deposited, as those crystals of calcium oxalate so frequently seen in the tissues (Fig. 44, p. 61). *The supply of phosphorus is as phosphoric acid, phosphates being absorbed from the soil.* Culture experiments show that a supply of calcium phosphate is suitable.

From such materials, together with carbohydrate resulting from Photo-Synthesis, new proteid is constructed. It is uncertain where this takes place. Probably it may occur in the mesophyll of foliage leaves, but there is no reason to believe that it is restricted to that tissue. *The plant supplied thus with carbohydrate, and with proteid in increasing quantity, has at its disposal those materials which are necessary for the growth of its tissues and for the development of new organs.* It is thus seen that part of the carbohydrate produced in Photo-Synthesis may be used up in the production of proteid. A considerable proportion may also be used in supply of material for cell-walls, and in other ways. Thus the immediate needs of the growing plant for the production of new tissue are met.

STORAGE.

Since under favourable conditions Photo-Synthesis is a relatively rapid process, it will commonly happen that material is gained more quickly than it is used up. *The balance is then stored for future use.* It may be laid aside in ordinary normal tissues, and this is the usual condition. Any parenchymatous tissue may serve. For instance, in trees which drop their leaves in autumn and form a new suit of them in the spring, the material for these is prepared in the previous season, and stored in the trunk and branches. It is laid aside chiefly in the medullary rays and the wood-parenchyma, as well as in the parenchyma of the cortex. Accumulations of it may even be made for a series of years as in the Beech, which flowers only at intervals and then profusely, depleting the store. But in many cases, especially in herbaceous plants, storage is effected in parts specially distended for the purpose, as in the turnip, carrot, and potato, or in the swollen roots of the Dahlia; or, again, in the fleshy leaves of the Onion and other bulbous plants. Lastly, in seeds material is habitually stored, which is provided by the activity of the parent plant to meet the needs of the seedling in the first stages of germination. Storage, in one form or another, is then a common phenomenon in plants.

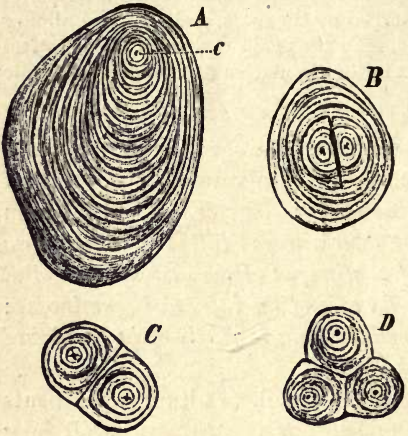


FIG. 77 *bis*.
Starch grains from the Potato. *A*, simple; *B*, half compound; *C*, *D*, compound grains. *c*, organic centre, or nucleus of formation. (×540.) (After Strasburger.)

The materials thus stored fall under three heads: (1) *Carbohydrates*, (2) *Fats*, (3) *Proteids*. The first and second of these are non-nitrogenous, and may be regarded more particularly as formative materials for cell-wall. Materials of the third class are nitrogenous, and may be held as more directly formative for protoplasm. The *Carbohydrate* appears most frequently in the form of Starch-Grains (Fig. 77); occasionally it takes the form of a cellulose thickening of the cell-walls, as in the Date stone and the seeds of other Palms (Fig. 78). These amyloid substances being insoluble are a compact form of storage. Carbohydrates may also be laid aside as Sugar (Sugar-Cane, Beet, Onion), or Inulin (Dahlia roots, Artichoke tubers), which being soluble substances are less compact, and are invisible in the living tissues; but either of them may be precipitated as crystals on extracting the water from the transparent tissues by alcohol. The *Fats* are commonly present in the form of large or small oil-globules in the protoplasmic body. Oil may also be distributed throughout the protoplasm, giving it a highly refractive appearance. Since carbohydrates are usually absent where oils are thus stored in quantity, it appears that the latter may serve physiologically as substitutes for the former. A good example is seen in the endosperm of the Castor-Oil seed, where starch is absent though it makes its appearance in the seedling. Oil is a very compact form of storage of combined Carbon. It has a higher percentage of Carbon than carbohydrates. Accordingly it is not uncommonly found in small seeds, where compactness of storage is essential. *Proteids* are frequently stored in the form of the dense protoplasts of the cells, as in the endosperm of Palms. But they may take definite form as *Aleurone Grains, or Crystalloids*. The latter are seen in the Potato (Fig. 79, *C*), where they have a very regular cubical form. Aleurone Grains are found in seeds, and are especially large where oil is also stored: as for instance, in the Castor-Oil seed, where they are oval in form, and contain within an amorphous outer proteid coat a crystalloid and a globoid composed of phosphates (Fig. 80). Such are the forms in which excess of nutritive materials may be stored. The chief interest lies in the insoluble forms of storage. Their deposit involves as a rule chemical change. For instance, sugar which is soluble and can readily be transferred by diffusion, may be changed into insoluble

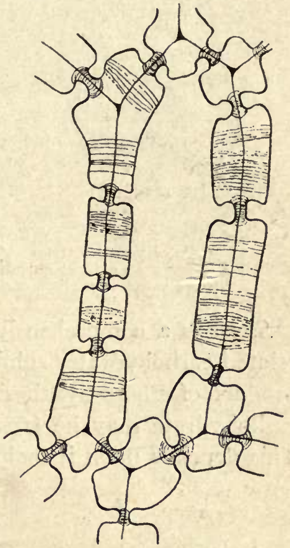


FIG. 78.
Cell-wall of a single cell of the endosperm of *Lodoicea*, consisting of storage-cellulose which forms the thickened regions of the wall. (× 400.) (After Gardiner.)

starch or cellulose, or it may be transformed into fats. In order to be again of physiological use these insoluble substances must be converted back into sugar. The *methods of storage and transfer of carbohydrates* may best be illustrated by the commonest example, viz. by the case of Sugar and Starch.

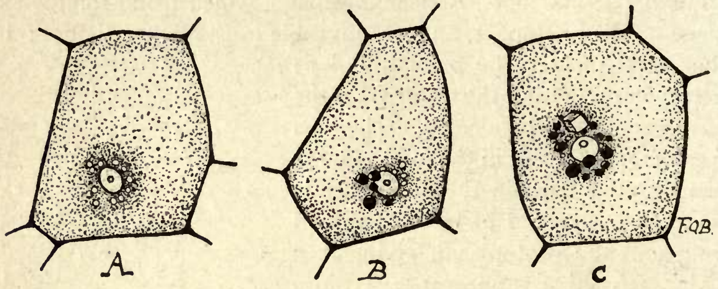


FIG. 79.
Cells of young Potato. *A*, with minute leukoplasts surrounding the nucleus. *B* shows some of these already forming starch, stained darkly with iodine. *C* shows further starch-formation, and one cubical protein-crystalloid. (× 220.)

Sugar is a comprehensive term which covers a number of closely related carbohydrates soluble in water. *Glucose* is probably the first product of Photo-Synthesis. Sugar is also the usual form in which carbohydrate may be transferred from place to place in the plant. This depends upon its solubility in water, through which medium it may move by diffusion. The tissues contain water of imbibition, and also fluid water; and though the living protoplasts are able to exercise control over movements by diffusion, nevertheless water as the ready medium of deposit, or of transit for sugar is constantly present. But soluble sugar is a bulky form of accumulation of carbohydrate, and being osmotically active, would in large quantities raise difficulties in relation to turgor of the cells. Consequently it is commonly converted into insoluble Starch, in the form of Starch-Grains. Such grains are not formed at large in the cell, but always in relation to plastids. These may be in the form of *green chloroplasts*, in which the included starch-grains make their appearance as the first visible result of Photo-

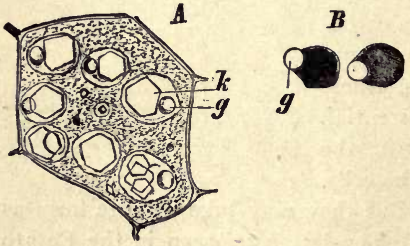


FIG. 80.
A, cell from the endosperm of *Ricinus* in water. *B*, isolated aleurone grains in oil. *k*=albumen crystals. *g*=globoid. (× 540.) (After Strasburger.)

Synthesis. Or they may appear as *colourless leukoplasts*, in cases where starch is formed in parts shut off from the light (Figs. 79, 81, *A-E*). Here the starch-grains are commonly of large size, and the leukoplasts being relatively small and colourless, they have frequently been overlooked. Nevertheless accurate observation has shown that *where starch is formed, either leukoplasts or chloroplasts are constantly present, and precede them. It thus appears that the capacity for converting sugar into starch resides in the plastids.*

But when the insoluble starch is again required for physiological use, it is converted back into sugar, in which form it can be transferred to the point where it is required. A movement through the tissues

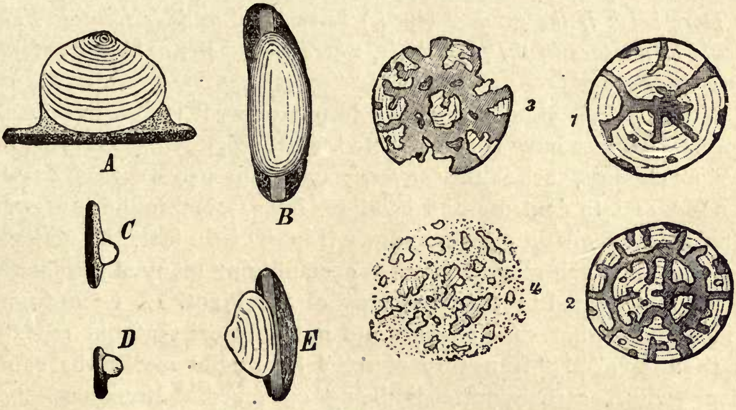


FIG. 81.

A-E, Leukoplasts from tuber of *Phajus*), showing various stages of development of starch grains. 1-4, Various stages of the corrosion of starch-grains in germinating Barley. (After Strasburger.)

would obviously be impossible for the solid grain. The change happens quickly in the case of the grains included in the chloroplasts, and a few hours in the dark suffices for their re-solution. The details of the change are best observed in the large storage-grains such as those of the Barley. It is found to depend upon the action of *Diastase, an enzyme or ferment widely distributed in plant-tissues* where starch is present, and is being used up: as in germinating grains. This substance can be extracted from tissues that contain it, by glycerine, and precipitated from the solution by alcohol. If the precipitate be collected and re-dissolved in water, a solution is obtained which still keeps its properties; but these are destroyed on exposure to a temperature of 75° C. By its reactions diastase is shown to have much in common with proteids. If a solution of diastase be added to starchpaste, made by heating starch in water, it soon ceases to give the blue reaction with Iodine; the colour given with Iodine changes to red, and finally to yellow. This indicates a change from starch to sugar (Dextrose). If starch-grains which have been digested in a solution of diastase be examined microscopically they are seen to have become corroded (Fig. 81, 1-4), while the solution gives the reactions of sugar. It is thus seen that *under the influence of diastase starch is converted into sugar.* What happens is hydrolysis, that is, the splitting up of the substance into smaller molecules, with the absorption of water. Into this process the diastase probably does not itself enter. It acts as a catalyser. *It is found that a very small quantity of the enzyme is able to convert a large quantity of starch into sugar, and that the action is more brisk if the product (sugar) be removed as it is formed. This would be the case in the plant-body, where the sugar would be constantly used up.*

Such enzyme-action is common in plants, as it is also in animals. Special enzymes have been extracted, and recognised as carrying out various changes, such as the conversion of cellulose into sugar (Cytase); cane-sugar into dextrose and levulose (Invertase); inulin into sugar (Inulase); or oils into carbohydrate (Lipase). In fact, the action of diastase on starch may be taken as exemplifying many of the changes intimately related to the physiology of the Plant. A circumstance which shows that such changes are not only existent but repeated is that so-called "transitory starch" habitually marks the course along which carbohydrate is being conveyed. Numerous small starch-grains are formed in the cells, and there can be little doubt that the conversion of sugar into starch, and again of starch into sugar, may be repeated over and over again. *Thus it is seen that in the metabolism of the plant chemical change is very active, and that the changes may be reversed. But in order to effect such changes as these, energy must be available.* The next question will be from what source does such energy come?

Respiration.

The readiest source of energy available for the ordinary purposes of man is by the combustion of fuel, such as coal or wood:—that is, its oxidation, the ultimate products being carbon-dioxide and water. The latent energy of chemical separation of the fuel is converted on combustion into kinetic energy. This supplies the motor impulse for engines of various kinds. In a somewhat similar way *the living organism, whether plant or animal, may transform energy of chemical* *separation resident in its carbonaceous materials into kinetic energy.* This may be exhibited in the movements, or other physiological changes which accompany life; while the final products may be, like those of combustion, carbon dioxide and water. For the combustion of coal a supply of free oxygen is necessary. The same is the case for the life of ordinary organisms, animal or vegetable. During life they also carry on a gaseous interchange. *Free oxygen is absorbed from the air, and carbon dioxide is evolved. To this interchange the term* RESPIRATION *is applied.*

The evolution of carbon dioxide by living plants is most readily demonstrated in the case of germinating seeds or of flowers, in which

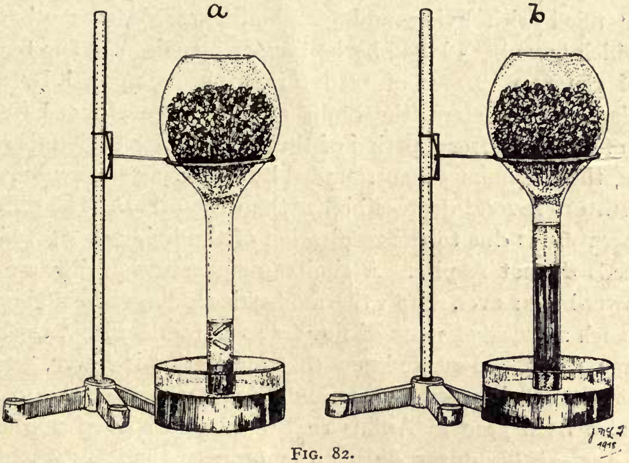


FIG. 82.
Arrangement for demonstrating Respiration. *a*, shows an earlier stage in the experiment: *b*, a later stage. See Text.

respiration is specially active. If a stoppered jar be filled about one third with germinating peas or wheat, the rest of the space being filled with atmospheric air, and left for say twelve hours, and the gas be then tested with a burning splinter of wood, the flame will be extinguished, showing that sufficient oxygen is not present to support combustion of the wood. The oxygen in the jar has been absorbed, and it has been replaced by carbon dioxide. But a more satisfactory demonstration of what has happened is given by the apparatus shown in Fig. 82. A globe connected with a long tubular neck is used. Into it a quantity of flower-buds are passed, the rest of the space being filled with atmospheric air. It is then fixed with the tube projecting downwards into a mercury bath. The buds are thus in a closed space from which oxygen may be drawn. A strong solution of caustic potash is passed into the tube over the mercury. As time goes on the level of the mercury will rise, until the volume of the gas has been reduced by about one fifth. *The oxygen of the air has been absorbed: in its place carbon dioxide has been given off, and as this is absorbed by caustic potash the volume of the enclosed gas has been diminished. The amount of the diminution gives a measure of the volume of oxygen absorbed.*

This gaseous interchange is essentially a process of combustion, comparable with the consumption of fuel. *A rise of temperature follows,* and this may be readily shown in the case of germinating seeds, or living flowers. Two thermos flasks are to be prepared, the one filled with living and germinating seeds, the other with seeds which have been killed by boiling, or by poison. The temperatures of the two masses of seeds are to be compared by a pair of similar thermometers, the bulbs of which are plunged into the middle of them. After a period of time allowed for the temperatures to settle, the thermometer surrounded by the living seeds will register a temperature several degrees higher than the other. The difference of temperature is due to the respiration of the living seeds, while the dead seeds do not respire. A similar demonstration may be given with flower-buds: even simple thermometric readings will suffice in the case of such a crowded mass of flowers as is found within the spathe of a large Aroid. Here we know that respiration is active, and it is now shown that it resembles combustion in the evolution of heat. It has also been seen in Aroids that accumulations of starch previously present disappear during the process. This represents the fuel that has been consumed.

The ratio of the volume of oxygen absorbed to that of the carbon dioxide given off in Respiration is not constant. In the case of ordinary green shoots the volumes are approximately equal. This may be expressed as the *respiratory quotient* $= \frac{CO_2 \text{ given off}}{O_2 \text{ absorbed}} = 1$. But it is not unusual in seeds, and especially in oily seeds, that a larger proportion of oxygen shall be absorbed during germination than of carbon dioxide given off. This is explained by the extra oxygen being used in the conversion of the highly carbonaceous oils into carbohydrate. Conversely, the volume of carbon dioxide given off may sometimes exceed that of the oxygen absorbed, and in extreme cases carbon dioxide may be eliminated without any oxygen being absorbed. This can only be a consequence of the breaking down of complex molecules, such as carbohydrate, with carbon dioxide as one of the final consequences. It may be readily demonstrated in germinating seeds excluded from the air.

If a few soaked and already germinating peas be passed up into an inverted test-tube completely filled with mercury, care being taken to exclude any bubbles of gas, after some hours gas will be found to have accumulated over the mercury, and it will continue to increase for several days. On testing, it will be recognised as carbon dioxide. This evolution of carbon dioxide without any absorption of oxygen has been styled *Intramolecular Respiration. Organisms showing it may be described as* ANAEROBIC, *as distinct from* AEROBIC *organisms, which live exposed to the air.* In the case of the peas it is an abnormal condition, and life under these circumstances is not long maintained in them. But there are many of the lower organisms which can exist indefinitely, and even normally in the absence of atmospheric air. They are called *anaerobic organisms*, and the most familiar of them is the Common Yeast, when actively carrying on fermentation at the bottom of a beer-vat.

Respiration is necessary in normal plants for active vitality, just as much as it is for animals. Successful germination depends upon it. Growth does not proceed without it. The movements, whether of the protoplast or of various members, as in the Sensitive Plant and others which show phenomena of movement, cease in the absence of a supply of free oxygen. In fact *respiration may be recognised as the normal means of liberating the energy which is required for carrying on the vital processes of the organism.* The absorption of oxygen, and the liberation of carbon dioxide may appear to be simple processes. But it is probable that these are only the first and last steps in very complex metabolic changes. Speaking generally these are changes of degradation : of breaking up of more complex molecules into simpler ones ; these changes, like those of combustion, end in carbon dioxide and water, together with an evolution of available energy.

It will be obvious that *Photo-Synthesis and Respiration involve opposite interchanges of gases*; *and particularly that in the former carbon is acquired from the atmosphere, while in the latter it is liberated. By the former the supply of organic material is increased, by the latter it is diminished.* But the former goes on only under the influence of light : the latter goes on constantly during life, independently of light. Accordingly, while respiration only will proceed during the night, both may proceed simultaneously during the daytime. It will then depend upon the relative activity of the two processes whether the plant gains on the whole, or loses in substance. It certainly loses by respiration during the night, or if kept in the dark. The young seedling also loses on germination before its green shoot is expanded above ground. The question will be whether the activity of Photo-Synthesis is sufficient to make up for the loss by respiration over the whole average day's work. *It has been estimated that one hour of active Photo-Synthesis will produce as much starch as would supply a loss by Respiration of about thirty hours. Thus there would be an ample balance on the whole day's work not only to prevent loss, but actually to increase the organic supply.*

For all practical purposes Photo-Synthesis in Green Plants is the source to which the origin of all other organic substances may be referred. This applies not only to the plant but also to the animal body. Any general observer will note the dependence of herbivorous animals upon their plant food, and the preying of carnivorous animals upon them. These are simple cases of physiological dependence. However complicated the steps of such physiological dependence may be, practically all organic life forms a continuous physiological chain, the initial link of which is Photo-Synthesis in the Green Plant. It is a process of deoxidation, and all Organic Life consists in the gradual breaking down again of the products of this deoxidation, till the starting points of carbon dioxide, water, and salts are again reached. A horse eating hay or corn digests its materials and evolves their stored energy in the form of work; while it gives off CO_2 and water in breathing, as well as urea and other matters which mark steps in the return of the materials of its food to the original sources.

On the other hand, when a plant or animal dies, the corpse may still contain a quantity of combined carbonaceous material. All of this is ultimately returnable in the course of decomposition to the initial forms of water, carbon-dioxide, and certain salts. Nevertheless there is nothing inherent in organic matter itself that leads to decay. Disorganisation of the dead body follows only as a consequence of the use of its constituent substances by other animals or plants to sustain their own life. These continue the process of destructive metabolism, by which the results of construction tend again to return to their original sources. But under certain circumstances decomposition may be arrested. Any organic material treated so as to exclude organisms that cause decay can be kept indefinitely. All "canned" foods depend for their keeping upon this perfect exclusion. The case is somewhat similar where the bodies of animals or plants are buried in mass under water-borne silt. They may then remain for ages incompletely disorganised, as *coal*. But when dug up the energy of chemical separation of the carbonaceous material, derived from the sun ages ago, may be again available in combustion for modern uses. The initial step of Constructive Metabolism appears to be taken quickly in the Green Plant exposed to the Sunlight. Destructive Metabolism may involve many stages of re-oxidation, and they may be spread over long intervals of time. Time is not really a factor in the process, as is shown by the coal we use daily, or by any hermetically sealed food that we consume.

These general remarks are, however, a digression from the study of the Plant. Returning to the Green Plant itself, its Constructive Metabolism provides new material. This is required in the first instance for the nourishment and growth of its several parts: that is for the *maintenance of the individual.* But secondly, it is required for the increase in number of individuals. The *propagation of the race* can only be carried out when sufficient material is at hand from which to form the new germs.

CHAPTER VIII.

GROWTH AND MOVEMENT.

ARTISTS style vegetable objects collectively "Still Life." But to the physiologist these words are contradictory, for he knows that *Movement* of some sort or another is the most notable evidence of active Life. In the Living Plant movements may be of various sorts: (i) *Molecular*, which cannot be seen except by the results, these becoming apparent as chemical change; (ii) *Movements of the Protoplast*: these are visible under the microscope, but not with the naked eye, and as they are confined within the cell-wall they do not alter the form or position of the cell as a whole; (iii) *Movements of the shoot or root as a whole, or of its parts.* These last movements are the most obvious, but as they are usually slow, time is necessary for their observation. They may be referred to changes in the constituent cells. One reason for their slowness is no doubt the fact that the protoplast of each cell, though it is the vital agent, is not so free to move as are the protoplasts of the animal body: for it is encysted by its cell-wall. Like the mediaeval knight its movements are checked by its protective armour. The Plant has sacrificed mobility for mechanical defence. Though movement is occasionally present in mature parts, it is in young and still growing parts that it is habitually seen. There is indeed a close relation between growth of the plant-body, or of its parts, and Movement. It will then be well first to enquire into the nature of *Growth* and the conditions which determine it, before passing on to the study of *Movement.*

GROWTH.

The most obvious sign of *Growth* is increase in size. But as applied to a living organism the term connotes something more intimate than mere enlargement. It has been seen in germination (p. 5) that growth involves transfer and change of materials, which cannot by any means be restored again to their original state. *Growth may then be defined as an increase in size accompanied by a redistribution of available material.*

The conditions under which growth is possible are the following:

(i) A supply of plastic material in the plant.
(ii) Opportunity for gaseous interchange.
(iii) A temperature between certain limits.
(iv) Turgor in the cells.

The growth which ensues when these conditions are fulfilled may affect any of the dimensions of the growing part. The most obvious is *growth in length*, as shown in stems or roots. But growth may also be in *thickness*: or both dimensions may increase together. In the body of the Higher Plant growth is not uniformly carried out in all parts. It is localised. Certain zones or regions of a stem or root may be growing, while other parts do not alter. The distribution of growth in length may be demonstrated in young herbaceous stems or in roots, by measuring off on them by a rule units of length from the apex downwards, and marking them with Indian ink. After a period of a day or so a comparison of these marks with the original scale will show that their distances have increased, but that the increase is not uniform. (Fig. 83.) The greatest elongation will be shown in the growing shoot at some point considerably below the tip, while it

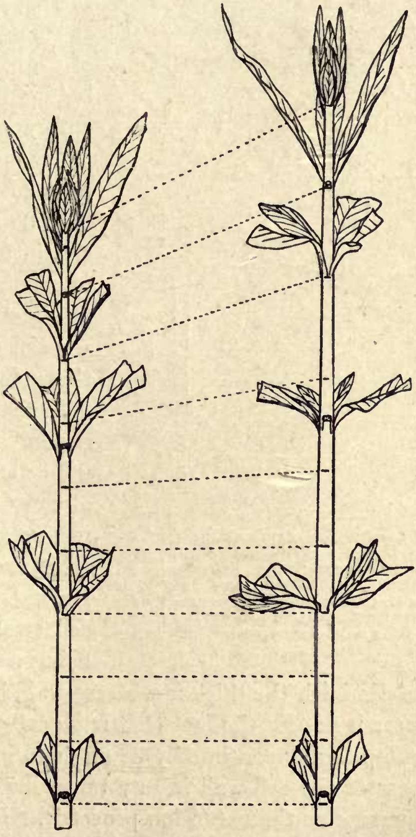


FIG. 83.
The left-hand figure shows a growing shoot at the beginning, the right-hand figure at the end of the period of observation. See Text. (After Errera.)

gradually diminishes on the one hand towards the tip, and on the other downwards, until a point is reached where it ceases altogether. This observation at once accounts for the general contour shown by growing shoots. In the apical bud the leaves are closely grouped because the axis has not yet extended to its full dimensions. The length of the internodes (or intervals between the leaves) increases downwards till their growth is complete, and their full length has been attained. Below that point the stem has become rigid, owing to general thickening of the cell-walls as they mature; and this naturally makes further elongation impossible. Thus the longitudinal *extension* of the tissues of a growing stem is a transitory state between the period of *initiation* in the embryonic region of the bud and the *mature* and *rigid state* seen in the lower part of the stem. Similar extension may be seen in leaves and in roots. In the latter it is found that the region of most active growth is within a few millimetres of the extreme tip. The zone of extension is much shorter than that usual in the stem (Fig. 84).

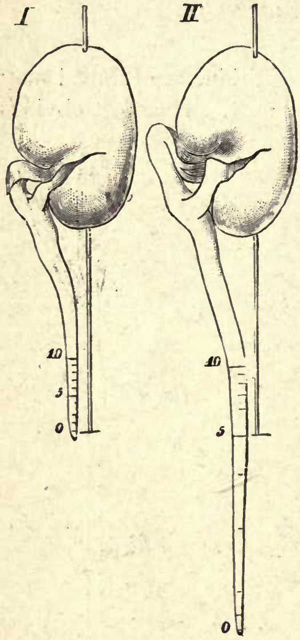


FIG. 84.

Localisation of growth near to the root-tip of *Vicia Faba*. In I. the root-tip has been marked with 10 zones 1 mm. apart. In II. the same root after 22 hours. The lines nearest the tip are now most separated owing to the growth having been there most active. (After Sachs, from Strasburger.)

Such extension of the whole part depends upon the growth of the individual cells composing it. It has been seen already (p. 21, Fig. 12) how young cells may elongate greatly as they mature, with vacuolisation of their cytoplasm. During the process the turgor of the cell stretches the thin cell-wall, which, being plastic, yields. This would tend to diminish the thickness of the wall, like a sheet of stretched rubber, were it not for the fact that fresh cell-wall-substance derived from the cytoplasm is continually being deposited. In point of fact the thickness of the cell-wall in any maturing tissue may be seen actually to increase as the extension proceeds. Its increase in substance, chiefly or perhaps wholly by apposition of fresh material to its surface, is actually more rapid than its thinning off by stretching. The walls are thickened by using up available materials, such as starch and sugar, which are converted into the layers of cellulose successively deposited. It is thus apparent how important in the process of growth are the conditions of turgor of the cell, and of the presence of available plastic material. The turgor depends ultimately upon sufficient water-supply, and upon the vitality of the protoplast, which again requires access of free oxygen for its maintenance.

The actual *rapidity of growth of the shoot or root as a whole varies* in different individuals, and according to external circumstances. In

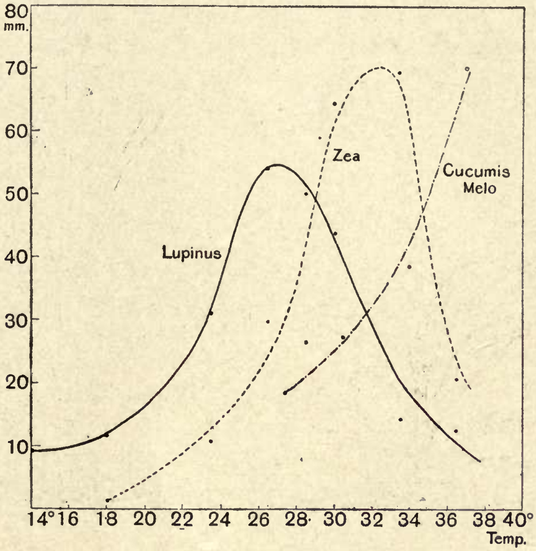


FIG. 84 *bis*.
Chart showing the relations of growth (in mm.) to temperature (in degrees Cent.), in the three seedlings named. The curves are similar, but the optimum, that is the crest of the curve, varies for different plants. It is higher for Maize and Melon than for Lupin. (After D'Arcy Thomson, based on observational data of Sachs.)

extreme cases it is sufficiently quick to be directly observed. Shoots of the Giant Bamboo grow in length over a foot a day, a rapidity that can be followed by careful observation with a lens. But as a rule growth is so slow that it is not readily apparent. Various mechanical arrangements by pulleys and levers have therefore been devised for amplifying and measuring growth when it is slow. These are termed Auxanometers. Combined with clockwork a recording auxanometer may be arranged, so as to give continuous readings of the rapidity of growth of a plant under observation. By these means the influence of external conditions upon growth, such as temperature, light, drought, etc., may be accurately studied.

It is a common fact of experience that *a rise of temperature from the normal accelerates growth.* Its influence in germination has already been considered (p. 8). In order to force plants on, the gardener cultivates them in hot-houses, or in frames slightly warmed by fermentative changes in rotting manure upon which the frames are placed. The rise of temperature in spring and early summer is a leading factor in the stimulation of growth at that season, while conversely the fall of temperature in autumn leads to a period of

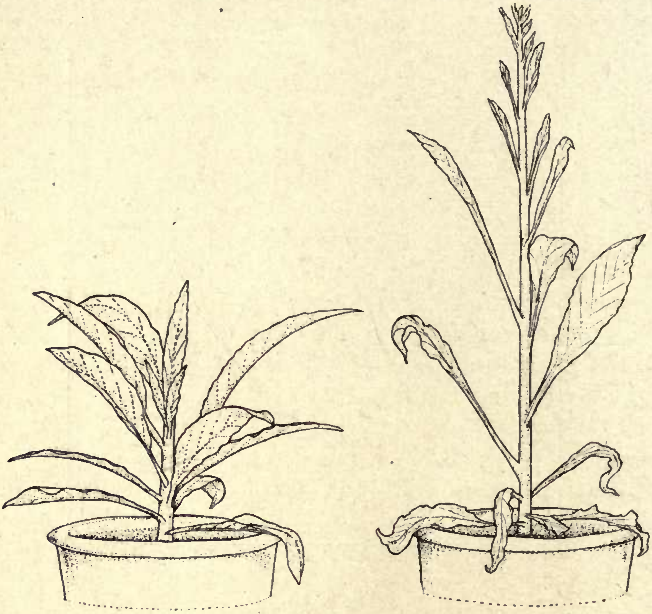


FIG. 85.
The plant to the left side is grown under normal conditions of lighting: that to the right is "etiolated." (After Errera.)

dormancy in vegetation at large. But there are limits of temperature outside of which growth will not take place. For most plants the *minimum* is about 0° C., and the *maximum* lies between 40° C. and 50° C. Between the minimum and the maximum, but as a rule nearer to the latter, lies an *optimum temperature at which growth is most rapid.* This optimum varies for different plants, but it is usually between 22° C. and 37° C., being lower for arctic and temperate plants than for those of the tropics. (Fig. 84 *bis.*) It may be noted for comparison that 37° C. is the normal temperature of the body in man.

Light has an opposite effect, acting as a retarding influence. If similar seedlings be grown at the same temperature, the one in light, the other in darkness, the former will show normal growth with a relatively short and compact form, and with expanded green leaves. The latter will show an abnormally elongated stem, while the leaf-blades are small, and the whole plant will be pale in colour. This condition is styled *etiolation*, and the length of the stem is due to the absence of the inhibitory influence of light. It has been found that the violet rays are the most effective, and that they have a retarding influence almost equal to that of full sunlight. (Fig. 85.)

It is the want of sufficient light for the normal development that makes plants in crowded greenhouses, or in dwelling-rooms grow "leggy," with unduly lengthened stems and leaf-stalks. Crowding of field crops has a like effect, and often leads to the "laying" of corn under heavy wind and rain before harvest, the plants being top-heavy and their stems weak.

Movement in Growing Parts

Any ordinary normal young shoot appears to be growing slowly but steadily forward. If the growth were equal on all sides the advance would naturally be steady, and in a straight line. Under casual observation this seems to be the fact. But if the growth be analysed by accurate observation it is found to be irregular. From time to time it is greater on one side than on another. The side where the growth is greater becomes convex, and the other concave. The apex will then appear to turn away from the side of greater growth, and a *movement will be the result. Such movements though small are the rule in normally growing parts.* They were first detected by Darwin in seedlings. By affixing a fine glass bristle, bearing at its end a small bead, upright upon the tip of a growing plant, and from time to time marking the position of the bead upon a horizontal glass plate placed above it, he obtained an enlarged record of the movements of the apex of the growing seedling. They were found to be slow, and

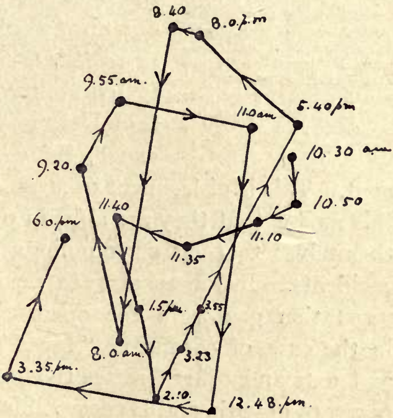


FIG. 85 *bis*.
Record of circumnutation in a seedling made by Mr. Malins Smith. Note that the direction was reversed at 8.0 a.m.

relatively minute. They were also seen to be irregular, and to circle roughly round a central point (Fig. 85, *bis*). To these movements he gave the name of *circumnutation*. They may be ascribed to variation from time to time in the relation of turgor to resistance of the cell-wall in the constituent cells. They record the sum of those variations. If the aggregate of them, on all sides of the organ, over a period of time such as a day, were relatively uniform, then the growth of the whole part would appear to be straight forward, as in normal stems. But however quiescent growing shoots may look, and however straight on they appear to grow, still it may be shown that they execute the slight and slow, but constant, movements of circumnutation. These movements are not dependent for their existence upon any recognised external stimulus. They are therefore distinguished as *autonomic*.

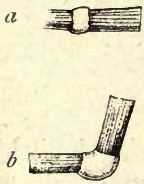


FIG. 86.
Single node of a Grass-haulm. *a* shows it horizontal, as it is after the grass is "layed" by wind. *b* shows it after unequal growth stimulated by gravity more strongly on the lower side, so that position is recovered.

But if any external cause were to upset this uniform aggregate of growth on all sides of the organ, and the rapidity of growth became unequal, a curvature of the whole part would result, and a movement of a more obvious kind than those of circumnutation would follow. The organism would thus show its *irritability*, being *susceptible to external stimulus*. Such movements of irritability are styled *paratonic*. If the external cause acts till the period of growth is ended, the curvature will itself become permanent. This is of frequent occurrence in growing plants, and it is by this means that they are able, in parts that are still young, to adjust themselves to their surroundings, and to recover from mechanical accidents. Instances of such recovery may commonly be seen in vegetation grown in the open. The most prominent example is in the case of cornfields "layed" by wind and rain. In wheat and oats and other Grasses the base of each leaf-sheath retains the power of growth, and is susceptible to the stimulus of gravity: so that the haulm can become again erect after it has been dashed to the ground (Fig. 86). *Reaction to the stimulus of gravity provides the best illustration of irritability.* Normally the plumule of the seedling grows upwards, and the radicule downwards, both parts showing movements of circumnutation. We have seen that this happens whatever the position of the seed may have been during germination. But if after this position has been assumed, the plant be placed with its shoot and root horizontal, the shoot by a curvature which is strongest at the region of most rapid growth, will resume its position pointing upwards, while the root turns downwards (Fig. 87). The growing parts thus readjust themselves in relation to gravity, and if then left undisturbed till growth stops, the curvatures become permanent. Such movements are styled movements of *geotropism*. Parts which curve towards the earth's centre are called *positively geotropic*; those in the opposite direction *negatively geotropic*.

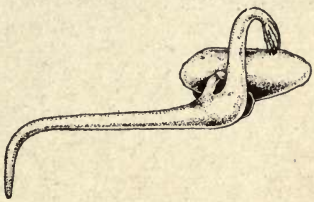


Fig. 87.

Seedling of Bean; after having been germinated, and the radicle had grown downwards and plumule upwards, its position was changed so that they were horizontal. The figure shows its recovery, the root having curved downwards, and the plumule upwards. The former is positively, the latter negatively geotropic. (Dr. J. M. Thompson.)

That gravity is the stimulating cause of the readjustment is indicated by experiments with the Klinostat, which is a clockwork arrangement for slowly rotating the plant during growth. If the plant be placed with its axis horizontal, and one slow rotation be completed in every quarter of an hour during the experiment, there will be no curvature, though gravity will have been acting on the horizontal shoot all the time. The explanation is that the stimulus of gravity, being distributed equally on all sides, they all react equally, and the part grows straight on. When seeds are germinated on the revolving klinostat the roots and shoots take haphazard directions, the influence of gravity upon them having been neutralised by its equal distribution on all sides.

In the case of the root it can be shown that the stimulus of gravity is received at the extreme tip, and that it is handed on to the point of most rapid growth, where the reaction takes place. It has been suggested that the stimulus is received by means of starch-grains, which are present in the tissues of the root-cap. (Fig. 87 *bis*, *A*, *B*, *C*.) These ponderable bodies may be seen to fall to whatever side of the cell is lowest. When the root points downwards, and they rest on the acroscopic side of each cell, no stimulus is received. The root is quiescent, and its growth is not disturbed. But if the axis of the root be so placed as to be oblique or horizontal, the starch-grains are seen to fall in a short time to that side of the cell that is lowest. Their presence in this unaccustomed position is believed to stimulate the protoplast. The stimulus is conveyed, probably by the continuous protoplasmic system, to the region of greatest growth, some distance back from the tip. There the equality of growth is upset, so that by greater growth on the upward side and less on the lower, a curvature is produced which restores the root-tip to its normal vertical position. Similar starch-grains to those of the root-tip are found in the tip of the cotyledon of certain Grasses which are also sensitive to gravity. The starch so constantly found in the endodermis of young stems is believed to serve a similar purpose in relation to the geotropic stimulus received in the stem. If the fact be as suggested, then the movements of geotropism provide an example in Plants of Stimulus and Reaction. Further, there is a localisation of the reception of the stimulus, and also of the conveyance of that stimulus from the point where it is received to the point where reaction appears. The analogies with the behaviour in the Animal body are obvious.

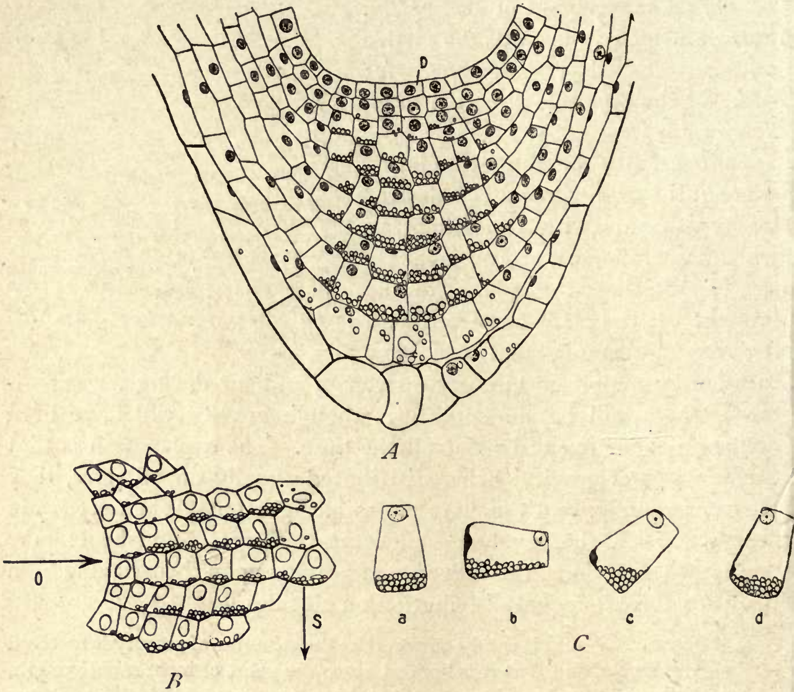


Fig. 87 *bis*.

A. Median longitudinal section of the root-cap of *Roripa amphibia*, showing starch-grains settled to that side of the cells which was lowermost. *D* = dermatocalyptrogen.

B. Tissue of root-cap of *Helianthus annuus* after 24 hours in a horizontal position. Arrow (*O*) shows axis of root. (*S*) shows direction of gravity.

C. Diagrammatic representation of the perceptive cells of the root-cap of *Pisum sativum*. *a*, at rest; *b*, 30 minutes in horizontal position; *c*, *d*, in course of reaction, to show the shifting of the aggregation of protoplasm.

(After Nemec.)

Even the use of ponderable solid starch-grains has its parallel in the otoliths of the Crustacea. But whatever opinion may be held as to the validity of this theory of perception, finally the phenomenon of response is relegated back to the living protoplast, to which the ponderable bodies are merely the means of conveyance of the stimulus of direction.

It is a familiar fact that when Plants are grown in a room having a window lighting it on one side, the leaves and shoots grow towards the light. Roots as a rule react in the opposite sense, turning away from the source of light, when they are exposed to it. This converse reaction of root and shoot may be seen with special clearness in seedlings grown floating on water, and lighted only from one side (Fig. 88). Such reactions are described as phenomena of *Heliotropism*. The parts which curved towards the light are styled *positively heliotropic*, those which curve away from it *negatively heliotropic*. But shoots of some plants are negatively heliotropic. The climbing shoots of the Ivy, and especially the tendrils with attachment-discs of the Virginia Creeper, which are in fact shoots specialised for climbing, turn from the light. By so doing they approach the tree-trunk or other support. Thus positive heliotropism is not inherent in all shoots. Other parts dispose themselves so as to offer the flattened surface to the incidence of light. This is so with most leaves. The curvature leading to this result is styled *transverse heliotropism*. But again, this is not characteristic of all leaves. The mature Gum-Trees of Australia have their leaves twisted so that they are expanded in a vertical plane, though their seedling leaves are disposed as usual (Figs. 3, 4,).

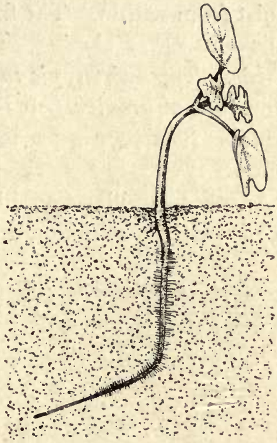


FIG. 88.

Seedling of Cress, germinated with its root in water, and exposed to oblique lighting from the right. The shoot shows a curve of positive, and the root of negative heliotropism. (Dr. J. M. Thompson.)

The heliotropic reaction appears as before in the zone of most rapid growth, and it consists in an inequality of the rapidity of growth on the sides of the part towards and away from the source of light. It is less certain here than in geotropism exactly how or where the stimulus is received It has been suggested that the prevalent convexity of surface of the superficial cells of stem or leaf makes each cell act as a condensing lens, concentrating the light upon the receptive protoplast. There is no doubt that the cells do so act, for photographs of various objects have been made, using epidermal cells as lenses. Moreover, certain modifications of superficial cell-walls are consistent with specialisation of this lens-character, and are held to support an "ocellar" theory. Whether or not this is the right explanation of the receptivity in Heliotropism, the ultimate receptive body is, as in geotropism, the living protoplast.

A common occurrence in the country is that drains of porous tile are stopped by invading roots of neighbouring trees. It sometimes happens even to leaden pipes when defective. The roots make their way through the soil to the source of water. That moisture exercises a directive influence on the growth of the root may be shown by germinating seedlings on the outer rim of a porous flower-pot kept moist from within. The first roots, growing over the edge of the pot, follow its outer sloping surface, instead of growing vertically downwards. The *hydrotropic influence* of the moist surface is here stronger than that of gravity. It is this hydrotropic curvature of roots which explains how they grow towards, invade, and choke porous or leaky pipes.

Another familiar fact illustrates the sensitiveness of living plants to a further stimulus, that of the free access to atmospheric air. When plants are grown in porous earthenware pots, especially if they are left too long in small pots without re-potting, the roots form a dense mat close to the inner surface of the pot. Such plants are described as "pot-bound." This condition is due to the fact that the roots grow towards a source of free oxygen. The pot is porous, and allows of gaseous interchange with the air outside. Such a response is styled *aerotropism*, and roots curving towards the source are *positively aerotropic*. The opposite is, however, seen in pollen-tubes (see Chapter XVI.). If pollen-grains be cultivated on a slide in a suitable sugar solution, under a cover-glass, the resulting pollen-tube curves away from the margin, where they would be subject to free aeration, thus showing *negative aerotropism* (Fig. 89). In this case the reacting body is a simple non-septate tube. Thus an undivided protoplast may be irritable, receiving and reacting to external stimulus, and modifying its growth accordingly. Such *examples of irritability* as these described, either in simple or complex parts, are *all referable to the living protoplast, and involve movement in growing parts.*

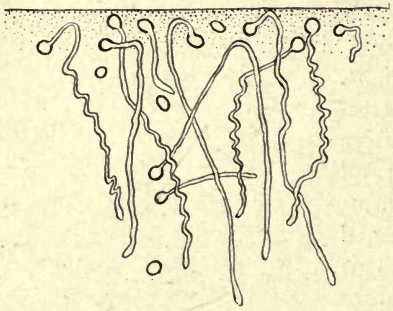


FIG. 89.
Pollen-grains germinated in a nutritive medium under a cover glass, of which the margin is shown. The tubes curve away from the margin, that is, away from the supply of oxygen. (After Molisch.)

But on the other hand, external stimuli, if their action be continued during growth till the rigidity of the mature state is attained, may leave a permanent, and often a profound effect upon the final form.

Two factors may be recognised which co-operate in determining the contour of the developed Plant. One is *the mode of growth inherited from the ancestry.* This is no doubt the chief and decisive factor determining plant-form. It provides those distinctive characters by which organisms are recognised and classified. But an important second factor is *the impress of the environment during growth.* Changes of form and proportion may be induced by external influences which, though they are not heritable, may appear very profound. They are styled *fluctuating variations.* They may in extreme cases so modify the vegetative development of the individual plant, that there may be some difficulty in allocating it to its true systematic position till its propagative organs have been examined. This applies especially in the case of amphibious species, such as the Water Buttercups in which the submerged leaves differ greatly in form from those developed in the air.

Movements in Mature Organs.

Movements also occur in mature parts, though not so generally as in growing organs; and perhaps they are less distinct from these in their nature than they seem to be. They also are directly referable to stimulation of the protoplast. But the reaction depends upon *changes in turgescence of the mature cells, accompanied by shrinkage, followed by recovery.* The Sensitive Plant (*Mimosa pudica*) is a notable example. It is a shrubby tropical weed, with doubly pinnate leaves, which show obvious changes of position of the leaf and segments according to circumstances. They, in common with the leaves of many other Leguminosae such as the Common Clover, change their position before night-fall, and at daybreak, assuming what are called the *night and day positions.* During the day the leaf-stalk is erect, with all its leaflets widely expanded in a horizontal plane (Fig. 90, *I*). But in the evening the pairs of leaflets fold their upper surfaces together, the pinnae instead of radiating widely, narrow the angles between them, while the petiole falls from the erect to a pendent position. In fact the whole appearance of the shoot alters (*II*). These changes come about by a hinge-like action at the base of each segment or pinna, and of the leaf-stalk itself. The vascular tissue is there contracted to a compact strand, surrounded by a broad cortical tissue with cellulose walls and active protoplasts, which is the motor tissue. The changes depend upon the turgescence of these cells. When a difference of turgescence occurs so that it is greater on the lower side, the hinge is raised: if it is greater on the upper side the hinge is depressed. This appears to be the mechanism of the so-called "Sleep-Movements" of the Leguminosae, Wood-Sorrel, and various other plants.

But the point which gives the *Sensitive Plant* its name is that it *also executes movements of a like nature in response to mechanical shock.* The disturbance of walking roughly through a patch of *Mimosa pudica* leaves a broad track of completely transformed vegetation. But if the stimulus be applied gently, steps in the change can be observed.

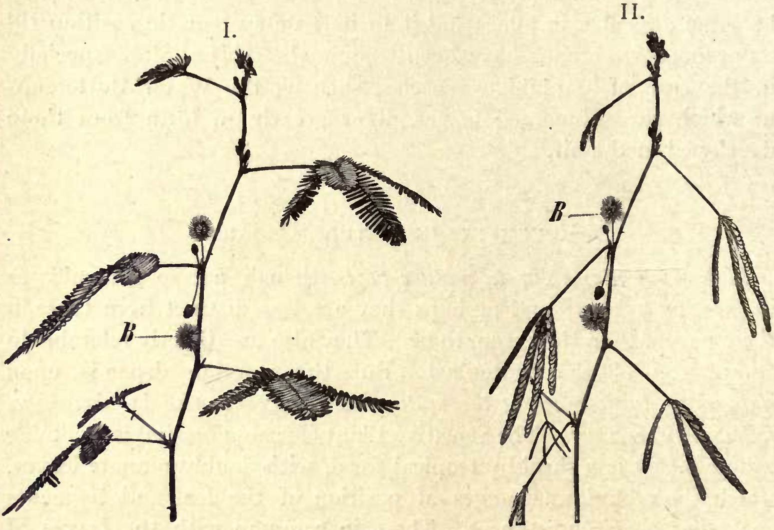


FIG. 90.

Shoot of *Mimosa pudica*. I. with leaves in the normal day-position. II. in the night-position assumed at dusk, or after stimulation. *B*=inflorescences. (After Strasburger.)

A gentle touch at the sensitive lower surface of the hinge at the base of the petiole makes the whole leaf fall, and the stimulus may then be extended outwards to the pinnae and successive pinnules. Or if the distal pair of pinnules be pinched, or stimulated with the hot head of an extinguished match, the stimulus received distally will extend downwards. The pinnules will fold in successive pairs, and finally the leaf as a whole will fall. If the stimulus be strong it may extend along the stem to other leaves. There may thus be *a conveyance of the stimulus to a distance.*

The movement following on shock is in the first instance due to stimulus of the protoplasts of the turgid cells, resulting in their loss of osmotic control, and water filters out into the intercellular spaces. The turgor of the cells on the sensitive lower side is thus diminished, and the hinge falls. Protoplasmic continuity has been demonstrated between the active cells of the hinge, which probably serves to convey the stimulus to them all (compare Fig. 19, *A*, p. 31). But this will not explain its transmission for the longer distances in the leaf; nor its further conveyance from leaf to leaf of the shoot. A specific tissue is believed to carry this out in a purely mechanical way, not as a protoplasmic excitation. Long thin-walled tubes, filled with sap surrounded by a delicate protoplasmic layer, are found in the phloem of the Sensitive Plant.

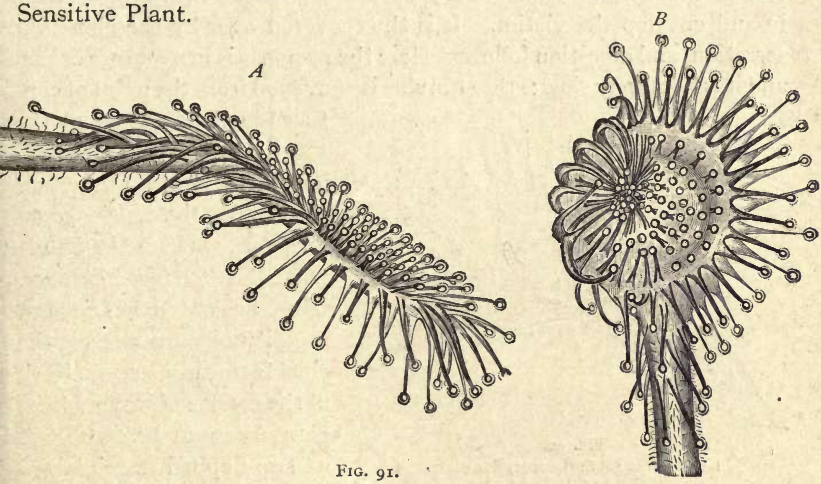


FIG. 91.

Leaves of *Drosera rotundifolia*; enlarged. *A*, in the receptive state before stimulation. *B*, after stimulation, viewed from above, with tentacles partly incurved. (After Darwin.)

These are held to serve as the channels of the conveyance of pressure-waves, consequent upon the movement in the hinge where the stimulus was first received. The passage of waves of pressure along a rubber tube filled with water can easily be illustrated; if one observer pinches one end of the tube, the stimulus is felt by an observer at the other end. Either positive or negative waves of pressure may thus be transmitted. It is believed that the stimulus in the Sensitive Plant is conveyed in this way, as a negative wave of pressure. If this be true the conveyance of the stimulus to a distance in the Sensitive Plant would not involve any specialised tissue comparable with the nerve of the animal body.

The most sensational movements seen in Plants are those connected with the Carnivorous Habit, as in Sundew (*Drosera*) (Fig. 91), or Venus' Fly-Trap (*Dionaea*) (Fig 92). These plants show elaborate though different mechanisms for the capture of insects, which are subsequently digested, and the materials absorbed as nourishment. In the former the action is slow, in the latter its success depends upon rapidity. *Drosera* bears on its spathulate leaves numerous radiating tentacles, each terminating in a spherical gland, which secretes a viscid juice. (Fig. 91.) This acts like birdlime, detaining any small insect that touches it. The contact-stimulus, confirmed by chemical stimulus from substances dissolved, is conveyed to other tentacles than those first touched, and movements of curvature result, so that the tentacles close in and envelop the victim. It is thus covered over by the glandular secretion, and digestion follows. Here the response is in a mature organ, and it is relatively slow; the stimulus is conveyed from the point of contact to a distance, where the reaction takes place, as a temporary curvature of the tentacles. But the *exciting cause is contact, confirmed by the presence of a digestible substance.*

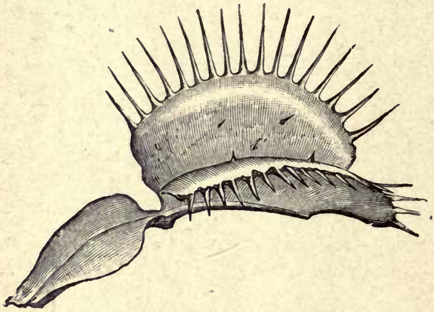


FIG. 92.
Leaf of *Dionaea* in the receptive state. (After Darwin.) (× 4.)

In the case of *Dionaea*, rapidity of movement is the chief factor in success. Each of the rosette of leaves of the plant bears at its distal end a two-flapped mechanism, like the covers of a book, mobile along the median line as a hinge (Fig. 92). The flaps are furnished with marginal spines, while three sensitive bristles rise erect from the upper surface of each. A touch on any of these six bristles sets the mechanism in motion. If conditions of temperature be favourable the flaps suddenly close together. An insect touching them would be captured within the trap; and as the inner leaf-surfaces are furnished with secreting glands, the digestion follows, with absorption of the soluble substances of the insect-body. Here the stimulus applied at the tip of the bristle is amplified by mechanical leverage, which compresses certain thin-walled cells at the base of each bristle. These are the actually receptive cells. From them the stimulus is rapidly conveyed to the reacting tissue of the hinge.

In all the cases described the living protoplast is the ultimate instigator of the movement. It may act from inner causes, setting up movements which are styled autonomic, such as those of circumnutation. Or it may be stimulated from without, as in the various paratonic movements. A reasonable probability may even be established as to the way in which the stimulus reaches the protoplast, as in the statolith-theory of starch-grains. But still the living protoplast is the active agent.

There is, however, *another class of movements in Plants which stand in no direct relation to the living protoplast.* Some of these depend upon the hygroscopic qualities of mature cell-walls, which swell unequally with moisture. This is seen in the awns of certain Grasses, such as *Stipa* ; or in the peristomes of Mosses, which twist with screw-like movements under changes of the degree of moisture in the air (see Chapter XXII.). If tissues composed of such twisting cells are closely related, as in a woody fruit, strains may be generated as the fruit ripens, which may be relieved by sudden rupture. This is seen in many explosive fruits, such as the Hairy Bitter-Cress (*Cardamine hirsuta*) (Fig. 93.) A very notable example of this is seen in the Sand-box Tree (*Hura crepitans*), the fruit of which explodes with a report like a pistol-shot, and throws the large seeds out to a distance of many yards (Fig. 94). Other cases of movement are due to changes in the volume of water in the cavities of special motor-cells, usually of diminution due to evaporation, resulting in their change of form. This is well seen in the annulus of Fern sporangia (Fig. 95), which curves backwards as its cells dry, but recovers with a sudden jerk, throwing out the spores. A somewhat similar explanation is given for the case of many Grass-leaves, which curl up under conditions of drought, but uncurl when water is plentiful (see p. 156). All such movements appear to spring from physical rather than from vital-physiological causes.

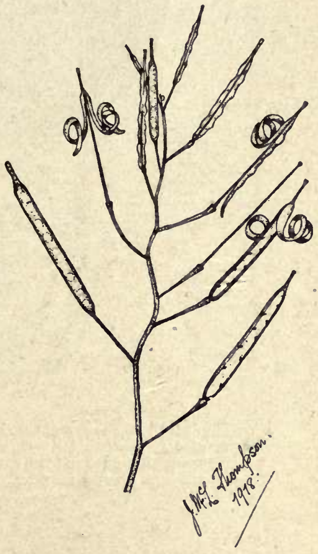


FIG. 93.
Fruits of *Cardamine hirsuta*. The uppermost are unripe. Those below them are ripe, and the carpellary walls, splitting away from below, curve so quickly as to throw the seeds forcibly outwards.

The movements seen in Plants are thus varied in their character as they are also in their biological effectiveness. Undoubtedly the most important, as they are also the most general, are the movements of growing organs, which are slow in action, and take their origin in variations of the osmotic turgor of the living cell, and of the resistance

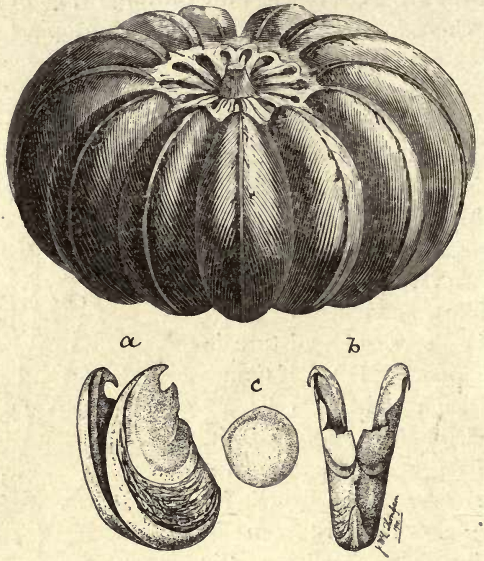


FIG. 94.

Whole fruit of *Hura crepitans*, before rupture of its woody carpels (after Le Maout.) *a*, *b*, single carpels after the explosion, showing each coccus with gaping halves. The rupture happens suddenly, each coccus taking a wider shape; the cocci and seeds are thus thrown asunder. *c*=a single large seed.

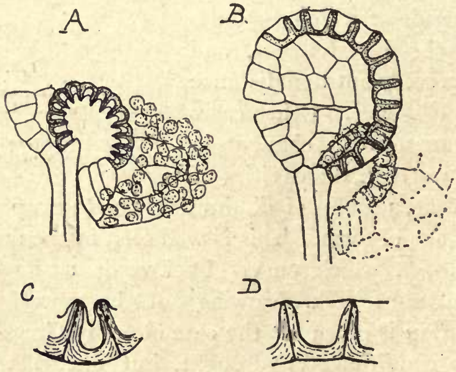


FIG. 95.

Fern sporangia: *A*, with the cells of the annulus darkly shaded, and curved strongly backwards by drying of its cells. *B*, the annulus after its sudden recovery, while the previous position is shown in dotted lines. *C* shows in detail cells of the annulus in *A*, and *D* shows similar cells in the state seen in *B*. See Chapter XXI.

of the cell-wall that holds it in. All of these phenomena of movement in growing parts play within the limits of turgor of the constituent cells, and it is structurally impossible that their mechanical effects should exceed, as they mostly fall short of, the limit of the pressure of the protoplast upon the containing walls. Such movements of the plant-body are brought about in an essentially different way from those positive contractions of muscle-fibres, which are the source of movement in the animal body. In this, as in so many other features, the two kingdoms show evidence of their initial divergence. However parallel their behaviour may appear to be, when fully analysed it becomes apparent that it is analogy, rather than any closer correspondence, that holds between them. For we do not find that either contractile muscular fibres, or a specialised nerve-system exist in the body of the Plant. Such movements as Plants show, and even the conveyance of stimuli, are brought about without them.

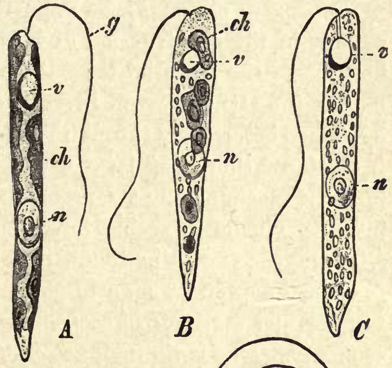
CHAPTER IX.

THE MECHANICAL CONSTRUCTION OF THE PLANT-BODY.

The texture of any normally growing Plant is relatively firm and elastic, so that it keeps its form, and after yielding to pressure tends to recover. Even young shoots show this; but it is a much more prominent feature in older plants. Woody trunks, large leaf-stalks of Palms, and old roots consist of hard masses of resistant tissue. They also may yield to the pressure of the wind, and they recover very perfectly after it is over. But if the limit of elastic recovery is passed, any part, young or old, may be so damaged that it is of no further use to the plant. A trunk may be shattered, a limb or a leaf may be severed, and so lost; or soft cells may be crushed between harder tissues, as may be seen in any leaf-blade roughly folded at too sharp an angle. To minimise such risks it is necessary that plants shall be mechanically constructed so as to resist those stresses and strains which are likely to befall them in their ordinary course of life.

Individual plants often attain large size. The Brown Tangles of the colder oceans may be 300 feet or more in length. Their leathery body is anchored to rocks, and buoyed up by sea-water, though exposed to its currents and waves. To maintain the form and attachment of so large a plant offers a quite considerable mechanical problem, which is shared by other water-plants in proportion to their size. But the requirements in the case of aerial plants are much more exacting, for they are not buoyed up by the medium in which they live. They must be stiff and firm of texture. Forest trees grow upwards to a height sometimes of 300 feet or more, and there hold aloft the dead weight of branches, leaves, and fruits. Not only must this be done in still air, but they must also be ready to resist successfully the impact of winds. In large plants this presents a serious engineering problem, and especially so in view of the fact that a perfectly elastic recovery after the wind-pressure ceases is a condition of its successful solution. A similar mechanical problem, varying with the size, presents itself in relation to every living plant that grows in the air. *The solution of such problems is based upon the fact that the cells forming the plant-body are encysted.* The necessary firmness which they show depends, in one way or another, upon the fact that a cell-wall surrounds each soft and slimy protoplast.

FIG. 96.



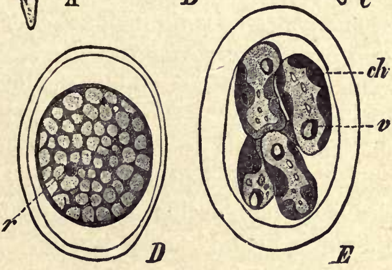


FIG. 97.

Euglena gracilis. *a*, Flagellate, showing in *A*, *B*, *C*, the motile condition, without cell-wall. *D*, is a resting cyst, with cell-wall. *E*, shows a cyst germinating. (Highly magnified.) S.

There is reason to believe that the evolution of multicellular plants started from simple unicellular beginnings. Those primitive creatures, the Flagellates, of which *Euglena* is an example, may be regarded as illustrating at the present day the sort of organisms from which the evolution of the higher forms may have started. *Euglena* shows two phases in its life: an active phase of motion, in which the plant exists as a primordial cell, that is, as a protoplast without a cell-wall. (Fig. 96, *A*, *B*, *C*.) But there is also a second quiescent phase, in which the protoplast is encysted, that is, surrounded by a cell-wall. (Fig. 97, *D*, *E*.) It is probably from some such source as this that the evolution of the plant-body of all the higher forms originated. For the encysted state of *Euglena* corresponds structurally and mechanically to that of the cells composing the ordinary tissues of plants; and it has been seen that the whole plant-body, however complicated, is built up of such encysted cells or their derivatives (Chapter II.). But the primordial phase is still represented in sexual propagation. The cells directly involved in that process, even in Flowering Plants, are primordial cells, and in many of the lower forms they are still capable of movement in water, like the active *Euglena*. The primordial protoplast has the advantage of free movement, but it is mechanically weak. Its soft slimy consistency may suffice for small unicellular organisms; but it would be quite impossible to construct large plants from such cells without some means of mechanical strengthening, especially if they are to live in air. It is on the basis of the encysted state, strengthened and protected by cell-wall, that large plant-bodies have been made possible. But the mechanical advantage conferred by the cell-wall has been gained at the sacrifice of mobility. Moreover, the mechanical framework offers an obstacle to physiological activity, and this may sometimes be a serious difficulty. *The method of construction of the plant-body is thus a compromise between the need for mechanical strength, and for the carrying out of the vital processes.* That the result is in favour of the plant is shown by the success which vegetation has achieved.

Economy of material is as important in the construction of the plant as it is in the construction of bridges, or ships by the engineer. In both cases the material is costly, while the less of it that is used the lighter the structure will be. In the plant the material used has to be gained laboriously through Photo-Synthesis. The end to be reached is the formation of as large a vegetative system as possible. But it must be mechanically strong enough to maintain its form. Our chief interest will lie in seeing how plants use their material to the best advantage. It will be found that the methods of its use run parallel to those adopted by man to gain similar results. In plants there are two distinct methods of securing mechanical resistance together with economy. One is through *turgor of the cells*, the other is by the formation of *specific mechanical tissues.* The former plays the chief part while the tissues are young, the latter is effective in the mature parts of the organism. But in their action they are not distinct from one another. Both may be effective in the same part, and at the same time. For the dependence on turgor gradually passes over to dependence on the specific mechanical tissues, as the shoot develops and its requirements become greater.

Rigidity as based on Turgor.

The fact that *living cells are normally turgescent* has already been discussed in Chapter II. The firmness and rigidity of the tense cell was there compared with the condition of an inflated football, or of a pneumatic tyre. The elastic cellulose wall corresponds to the outer cover, and the protoplast to the bladder, or to the inner tube. The withered or plasmolysed cell loses its power of mechanical resistance like a punctured tyre, or a deflated football. This condition holds for every normally living encysted cell while young, whether isolated as in some Algae, or forming a unit of some larger structure.

In the evolution of the higher forms from simpler organisms it might appear that the simplest way of extending the plant-body would be to enlarge the single cell as a non-septate sac. The best of this simple but ineffective method has been made by the Algal family of the Siphoneae. But it is only under favourable conditions that it can succeed, for it is obviously a weak method of construction. Unless buoyed up by water it is unsuitable except in the case of small organisms. Some relatively small members of the Siphoneae, such as *Protosiphon* or *Vaucheria*, live in damp situations exposed to the air. But all the larger forms are submerged, and live usually in still lagoons or pools. In *Valonia ventricosa*, which is a sea-weed, the

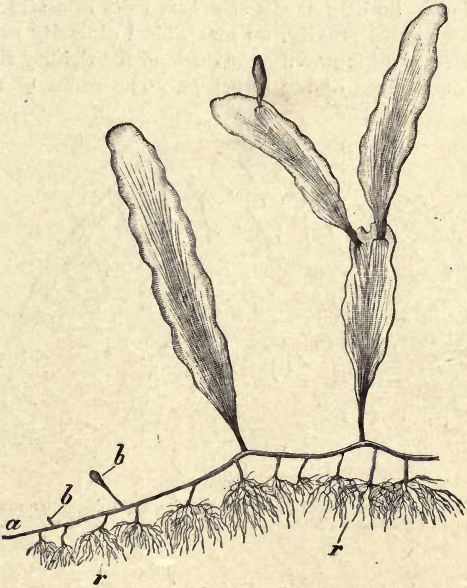


FIG. 98.
Caulerpa prolifera. *a*, growing apex. *b*, young thallus-lobes. *r*=rhizoids. Notwithstanding its elaborate form this plant is a single non-septate sac. (½ Nat. size.) (After Strasburger.)

form of the sac is simply spherical, or pear-shaped, and may be an inch or more in diameter. But in other genera it is more elaborate in form, and may extend to a foot or so in length. Some mimic curiously the creeping shoots of aerial plants; for instance *Bryopsis* and *Caulerpa* (Fig. 98). Many other of the larger forms, however, grow with numerous branches matted together, giving mutual support (*Codium*), or even cemented together into a solid mass by deposits of lime (*Halimeda*). Such structural modifications as these show that the non-septate sac is too weak a method of construction for practical use. It has only been adopted by a few organisms, the chief of which are certain Algae living in still water, a medium of nearly the same specific gravity as themselves. Thus buoyed up the action of gravity upon them is minimised.

If a spherical rubber balloon be filled with water so as to be turgescent, it keeps its form so long as it is submerged. But if it be lifted out into the air it changes its form according to the support, and the larger it is in proportion to the firmness of its skin the greater will be the deformation. A very large one with a weak skin will burst. These simple facts are in accordance with a general principle which rules for similar structures of various size. Their strength increases as the square of their dimensions, their weight as the cube of their dimensions. So long as the structure rests in a still medium, of its own approximate specific gravity, no mechanical difficulty need arise. But in a medium of less specific gravity the demand for rigidity rises in a higher ratio than the dimensions of the structure. The result of this applied to

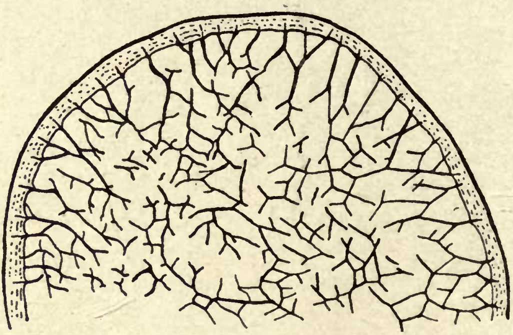


FIG. 99.

Part of a transverse section of *Caulerpa*, showing the thick outer wall, and the reticulate rods of cellulose, which act as ties, and give added rigidity. F. O. B. (× 50.)

plants is that a method of construction which suffices for small organisms, consisting largely of water, and exposed to the air, will not suffice for those of larger dimensions. The mechanical demand on the turgor and strength of the cell-wall in order to maintain form rises in a more rapid *ratio* than the size. *This is the reason why all large land-growing plants are septate*; also why land-growing Siphoneae are small, and the larger ones are all aquatic. In the case of the non-septate cell of large dimensions exposed in the air, the wall would have to be of such thickness in order to maintain the form of the organism under the influence of gravity, as to be on the one hand wasteful of material, while on the other it would present a formidable obstacle to physiological activity. Such thickening is seen in the large species of *Valonia* and *Caulerpa*, even though they grow submerged. In both of these genera the cell-wall is considerably thickened; but in the latter additional firmness is secured for the otherwise feeble structure by numerous cellulose rods, which stretch across the internal cavity, and act as ties (Fig. 99). In other large types some accessory means of strengthening has to be adopted, such as matting the branches together as in *Codium* and *Penicillus*: or cementing them together with lime as in *Halimeda*. These are to be regarded as concessions to the mechanical imperfection of the non-septate construction.

Cases of non-septate tissues exist in the body of some of the higher plants, but as they are embedded in other tissues they are not exposed to mechanical demands. Examples are seen in the latex-cells and vessels, as in the Euphorbiaceae and Cichoriaceae; and in the young embryo-sacs of the Flowering Plants.

All ordinary plants of large size are septate. This is specially necessary where they live exposed in the air, and are thus subjected to greater strains than if floating in water. In the embryonic region the cells are seen to divide into equal parts, the newer cell-wall

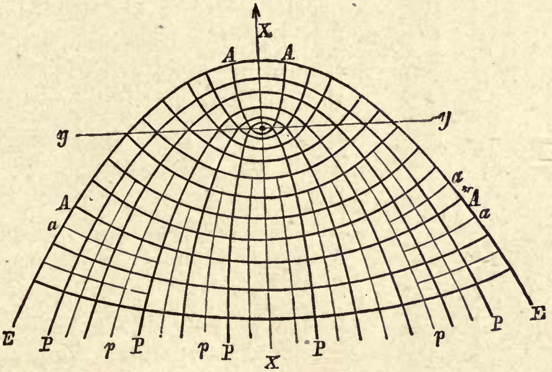


FIG. 100.

Diagram illustrating the plan of arrangement of cell-walls in the apex of the stem of an Angiosperm. *XX* = axis of construction. *EE* = external surface. *PP* = priclinal curves. *AA* = anticlinal curves. (After Sachs.)

being inserted at right angles on the older walls. This leads to a cell-net the exact detail of which depends upon the external form of the part (Fig. 100). The disposition of the walls is from the first such as to give added mechanical strength, but in the young cell the walls are extremely thin, and are composed of pliant material. In the young shoot the mechanical strength is almost entirely dependent on the turgor of the individual cells. When they are tense their walls do not act as mere props or stays, as do the floors or partitions of a house; but the turgor gives individual rigidity to each cell, and through them collectively to the whole part which they construct. A high mechanical effect is thus gained in a succulent structure with extreme economy of material. This may be illustrated by the case of the Lettuce. We have seen that a crisp Lettuce suitable for a salad gives by weight 96 per cent. of water, and only four per cent. of organic material for cell-walls and protoplasts. Such a structure is in fact a very slight organic framework containing water. The mechanical effectiveness of the internal turgor of the cells, and the insufficiency of mere partitioning of a young or succulent part is shown by comparing a crisp fresh leaf with one which has withered, or has been plasmolysed.

There is, however, another factor which increases the mechanical effectiveness of succulent parts in the young state, viz. the *mutual tensions of tissues.* If a fresh young stem of Sunflower or Elder, or any extending part of an herbaceous plant, be slit longitudinally into quarters, these take strong curves. The outer surface of each quarter becomes concave, the inner faces of each quarter convex. The curves become more marked after the cut stem has been steeped in water. These curves show that the relations of the tissues in the living stem are not passive. (Fig. 101, 2*a*, 2*b*.) That the phenomenon is one of turgor of the cells may be shown by allowing the slit stem to wither, or by plasmolysing it with a salt solution, when the curves disappear, and the parts become limp. On the other hand, if the several tissues be completely separated from a measured length of a fresh stem, and be themselves measured after separation, the column of pith will be found to have elongated, and the outer tissues to have contracted. To bring them back to their original state the pith would have to be compressed and the outer tissues stretched. (Fig. 101, *a*.) This is in fact their condition in the growing stem. The pith tends to elongate, but is held back by the outer and firmer tissues, which are thus kept tense. The relation of the inner and outer tissues is then analogous to that of the wall and protoplast in the turgescent cell, and the mechanical effect is the same. *It is thus seen that the firmness of succulent stems is due in large degree not only to the turgor of the individual cells, but also to the mutual tension of its tissues.* Similar relations hold for the tissues also of leaves and roots; but these need not be described in detail.

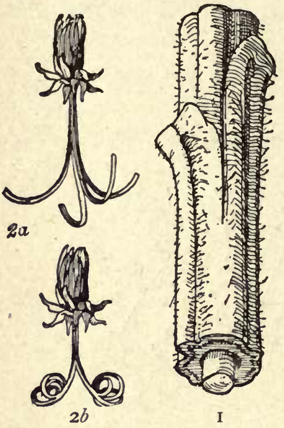


FIG. 101.
1, Shoot of Sunflower with pith separated by a cork-borer from the outer tissues. 2*a*, split stem of Dandelion. 2*b*, after immersion in water. (After Strasburger.)

Rigidity as based on Specific Mechanical Tissues.

Such methods serve to give the necessary mechanical strength to young parts. But as the tissues grow older, their walls become thickened. They are then less susceptible to turgor, as they are also more resistant to growth. Moreover, in the older parts the mechanical demand for support increases with the increasing burden of leaves and branches. These demands are met by *specific mechanical tissues*, fitted by their thickened walls to offer greater resistance. Though the effect of turgor is characteristic of young plants, and that of the specific mechanical tissues of the mature, there is no definite limit

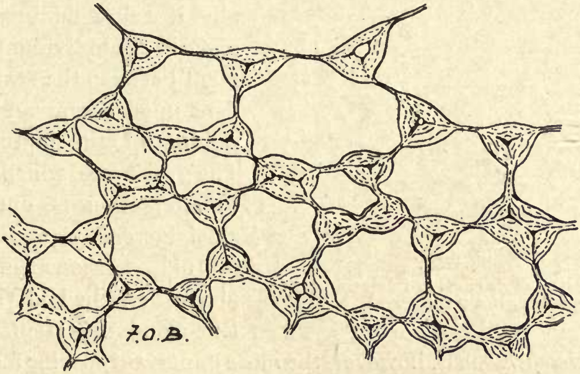


Fig. 102.
Collenchyma from stem of the Potato, seen in transverse section. (× 300.)

between the action of each. The dependence on the one merges gradually with age into dependence on the other, and in the growing part both sources of support may be effective at the same time.

There are two types of specific mechanical tissue, (*a*) *Collenchyma*, which is found in growing herbaceous stems and leaves; and (*b*) *Sclerenchyma*, which is characteristic of more mature parts. *Collenchyma* consists of cells which retain their living protoplasts, and thus remain physiologically active, while chlorophyll corpuscles are frequent in its cells. These cells usually have the form of 4-6-sided prisms, with transverse or oblique ends, and are sometimes transversely partitioned. The cell-walls are composed of *cellulose*, which is swollen in life with water. They are thicker at the angles of the prisms than at their flattened sides, where the thinner membrane allows of ready physiological interchange. This gives the tissue, when seen in transverse section, the appearance shown in Fig. 102. It is thus a tissue which, though mechanically effective, is not fully specialised for giving strength. The cells do not offer rigid resistance to elongation, but they themselves grow with the growth of the part they support, offering a persistent though plastic resistance. The position of the collenchyma is usually peripheral, closely below the epidermis. This gives it its full mechanical effect. In fluted stems it is usually massed at the projecting ridges, and between them it is often interrupted by thin-walled green tissue of the cortex. (Fig. 103.) Functionally it takes an intermediate place in the individual development between the state dependent upon turgor and the full rigidity of the mature state. The resistance which it offers to elongation is one of the chief factors in producing the mutual tensions of tissues above described in the succulent elongating stem.

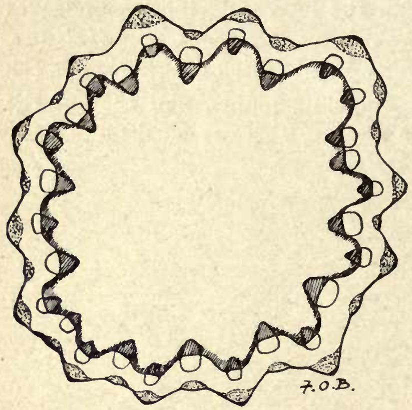


FIG. 103.
Flowering stem of *Astrantia* in transverse section. (× 10.) The collenchyma is dotted.

The *Sclerenchyma* is, however, the more important specific mechanical tissue. Its effectiveness depends partly upon its own characteristics, partly upon its distribution. It consists of cells with thickened walls, which are usually but not always lignified. When mature its protoplasts are no longer functionally active, and may be represented only by vestigial remains. It is then practically a dead tissue. The form of the cells varies. Sometimes they are cubical or oblong with square ends, and may be isolated, or disposed in groups. Such *stone-cells*, or *sclereids*, give a hard gritty texture to the parts where they occur, as in the bark or pith of various woody plants. The gritty nature of the fruit of the Pear is due to nests of such stone-cells. But frequently the sclerotic cells are elongated, and variously branched, as in the sclereids of the leaf of Tea, or unbranched with flattened ends, as in the leaf of *Hakea* (Fig. 104). Such cells are commonly isolated. They stiffen the parts where they occur by the resistance which their thickened walls offer to compression. The form, structure, and function of the sclereids of *Hakea*, which prop out the firm epidermis and thus give the leaf its remarkable stiffness, may be compared with that of the hollow steel columns used for supporting shop-fronts.

A more frequent, and mechanically a more effective form of strengthening cell is seen in the *elongated sclerenchyma-fibre*. Such cells are commonly associated in masses, often forming strands which run continuously for long distances. These strands of the Flax supply the material for linen, of the Jute for sacking, of Hemp, New Zealand Flax, etc., materials for cordage, while similar strands of the Coco-

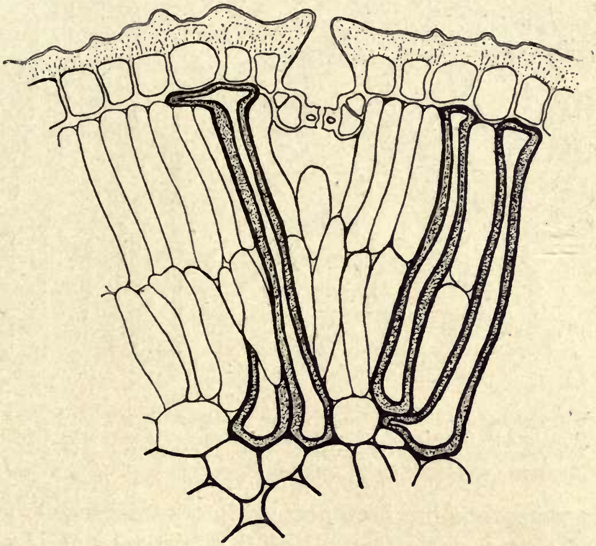


FIG. 104.
Part of a transverse section of the xerophytic leaf of *Hakea*, showing a stoma greatly depressed below the well-developed epidermis, which is propped out by thick-walled sclerotic cells. (× 150.) F. O. B.

Nut, and other Palms are worked up into mats, brushes, etc. In the plant they frequently accompany the vascular strands, and are often associated with the phloem as *bast-fibres*, or with the xylem as *wood-fibres* (compare Fig. 37). But there is no necessary association with vascular tissues, and the sclerenchyma is often quite independent of them. The mechanical cells themselves are elongated, with ends pointed and sides flattened, so that they fit closely together. (Fig. 105, *A*, *B*.) The cells of Hemp are about 100 times as long as broad, in linen the proportion is about 200 to 1; in the extreme case of the Rhea fibre (*Boehmeria*) the length has been estimated at 1500 times the breadth. The lignified walls may be so thickened that the cell-cavity is obliterated. They are thus practically rods of resistant material.

Each develops from a single embryonic, or cambial cell. As it elongates, its pointed ends slide between those of other fibrous cells, taking a sinuous course. The result is that the cells of the strand interlock, and when a longitudinal strain is applied, the resistant rods press laterally upon one another, so that the greater the strain the more closely are they united. Mechanically such strands act like solid metal wires.

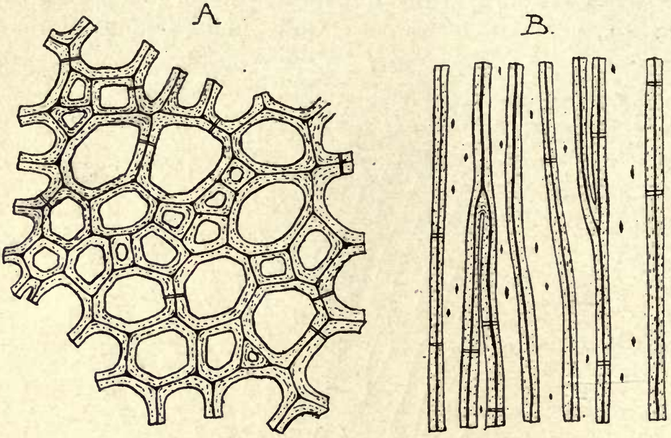


FIG. 105.
A, Transverse section of sclerenchyma of stem of Sunflower. The larger sections show cells cut through the middle of the fibre, the smaller near to the pointed end. *B*, the same in longitudinal section, showing the pointed ends of the cells. Small pits are present, in surface view, and in section. F. O. B. (× 300.)

This comparison has been pursued into measurements which bring out the characteristic features of the resistance of plant-fibres, as contrasted with those of certain metal wires of similar transverse section. The figures in the subjoined table show how different is the behaviour of the two under strain.

NAME.	Limit of Elasticity in Kg. per sq. mm.	Breaking strain in Kg. per sq. mm.	Elongation at limit of Elasticity per 1000 units of length.
Dasylirion - - -	17.8	21.6	13.3
New Zealand Flax - -	20	25	13
Hyacinth - - - -	12.3	16.3	50
Garlic - - - -	14.7	17.6	38
Nolina - - - -	25	..	14.5
Silver Wire - - -	11	29	..
Wrought Iron - - -	13.13	40.9	0.67
Steel - - - - -	24.6	82	1.20

The first column shows the maximum burden per unit of transverse section of the fibrous strand, or of the metal wire respectively, under which the *limit of elastic recovery* is not overstepped. The case of *Nolina* (25) is actually superior to steel (24.6). Other fibres compare favourably with silver and wrought iron. The second column shows the burden per unit of transverse section which causes rupture; that is, it states the *limit of tenacity.* It is seen that in this metals are distinctly superior. But the table brings out a very important feature of plant-fibres, that their limits of elastic recovery and of tenacity are very nearly coincident, while those of metals are widely apart. *Metals are ductile, fibres are not.* The importance of this in the plant-body lies in the provision thus made for *perfect recovery after strain.* Great breaking strength would be of no value if the plant subjected to the strain were permanently deformed.[1] The third column shows the *elongation* which the strand or wire suffers *at the limit of elastic recovery*, stated in terms of units of length per 1000 of the strand as a whole. Here the difference between the fibres and the wires is strongly marked, the fibres yielding in much higher degree than the metal wires. This again meets the requirements of a plant exposed to strains, such as wind. For *the tissues while resisting the strain very efficiently, yield to it, but recover very perfectly when the strain is removed.* This comparison shows that while metals have the superiority over fibres in tenacity, the fact that they are more ductile than fibres would unfit them for fulfilling the office required of mechanical tissues in the plant-body.

In late years metal straps have been used largely in concrete construction, reinforcing the concrete in which they are embedded. Ordinary herbaceous plants are constructed on the same principle. The sclerotic strands correspond to the metal straps, the surrounding parenchyma with its turgescent cells corresponds mechanically to the concrete. The office of the latter in either case is to keep the resistant straps in place, while the straps resist the tensions which would produce loss of form. In the reinforced concrete a high degree of rigidity is necessary, or the concrete would crack. But in the plant-

[1] Collenchyma is, however, exceptional. While its absolute strength is little inferior to that of bast fibres, its limit of elasticity is much lower: and it is thus liable to permanent elongation. But this is an advantage in growing stems in which it usually occurs; for it offers no rigid barrier to growth, while it is sufficiently resistant to meet sudden strains. It is like the Second Chamber in the Constitution of a State. It resists a new initiative: but if the initiative be continuously pressed, it yields. Meantime stability is maintained.

body, with its elastic cells and tenacious fibres, a considerable change of form is allowable in yielding to the strain without permanent injury following. The herbaceous plant thus has a distinct superiority over any building of reinforced concrete, for the embedding medium is itself elastic. The conditions are most nearly matched by the covers of certain motor tyres, where resistance must be coupled with elasticity.

In the economical use of material the *disposition of the specific mechanical tissues* is important, both on grounds of lightness of the structure, and the physiological expense of the substance used. The problem of obtaining the best mechanical effect with the least expenditure varies with the requirements to be met. *The girder principle*, which has been adopted by engineers as a means of securing a high degree of mechanical efficiency with economy of material, is frequently illustrated in the construction of plants. It is even seen in plants of the Coal Period, such as *Cordaites*, which lived ages before the origin of man. The common type is the double-strap girder, which gives in transverse section the figure (**I**). If a girder of such construction be fixed in the position indicated by the figure, and loaded in the middle while it is supported at the ends, there will be a tendency to curvature which will compress the upper strap or flange, while the lower strap will suffer tension. The resistance to these strains will depend upon the two straps being held rigidly in their relative positions by the connecting plate. The material will be most economically used if it be concentrated in the form of the upper and lower straps at the regions of greatest strain. The connecting plate may even be replaced in "latticed girders" by a system of connecting ties, which follow the lines of greatest strain. The wider the upper and lower straps are apart, consistent with their being held rigidly in place, the better the result will be. The principle is

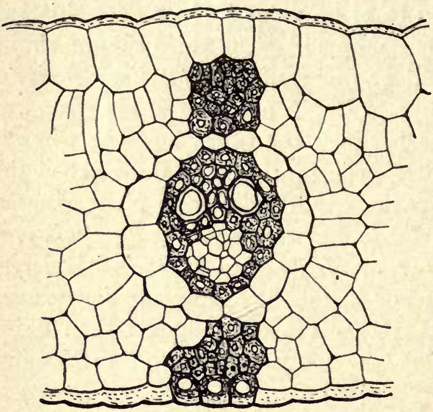


FIG. 106.

Transverse section through a leaf of *Cyperus*, showing a vascular strand with a strand of resistant sclerenchyma above and below, constituting a girder. (× 300.) F. O. B.

illustrated by the use of girders, or simple combinations of them, in the construction of bridges, floors, and shop-fronts. More complicated arrangements giving columnar construction are seen in lattice-signal-posts, and large gasometer-frames. The latter offer close analogies with certain types of stem-construction in plants.

In plants girder-construction depends upon differences of mechanical resistance of tissues. An illustration of a simple case is given in Fig. 106 from the leaf of *Cyperus*. On either side of the vascular strand there is a band of thick-walled resistant woody sclerenchyma. Each is close to the upper and lower surface respectively, indeed three cells of the lower epidermis are themselves sclerotic. These bands represent the upper and lower straps of the girder, while the less resistant vascular strand represents the connecting plate. The girder is kept in place by the softer tissues, but especially by the firm layers of epidermis.

The requirements that are most commonly illustrated in plants fall under three heads, which are typified by parts of normally growing plants, though they are subject to great variety with the varying form of the plant-body :

(*a*) Columnar requirement, as in an upright stem.

(*b*) Stiffening of flattened surfaces, as in the leaf-blade, and protection of the margins against tearing.

(*c*) Rope-requirement, as in roots of upright plants exposed to wind.

(*a*) The Columnar Requirement.

The *columnar requirement*, for support of the growing dead-weight of branches, leaves, and fruits, is met in large Dicotyledons chiefly by the woody column, which grows in proportion to the growing need for support. It is cylindrical, so as to meet all winds equally. It is composed of mixed xylem-tissues, with continuous woody walls. The most important of these mechanically are the wood-fibres, and the resistant quality of the wood is roughly in proportion to their preponderance. But all the tissues,—vessels, wood-parencyhma, and medullary rays,—contribute in varying degree to the mechanical effect. This is enhanced as the central tissues die, and are converted into heart-wood. The method of construction is that of the solid column, now acknowledged by engineers to be not the most economical of material. But in Dicotyledons the retention of this rather primitive method is to be explained as a compromise, the success of which is evidence of its fitness to meet the circumstances. For the living part of the growing trunk affords in addition to mechanical strength, room also for storage, and a means of transmission of materials.

In the stems of Palms, where a large terminal tuft of leaves has to be supported at a great height against winds, the mechanically effective tissues are massed towards the periphery, while the central regions are softer. This may be compared with the hollow metal column filled with concrete, which has the effect of preventing the metal skin

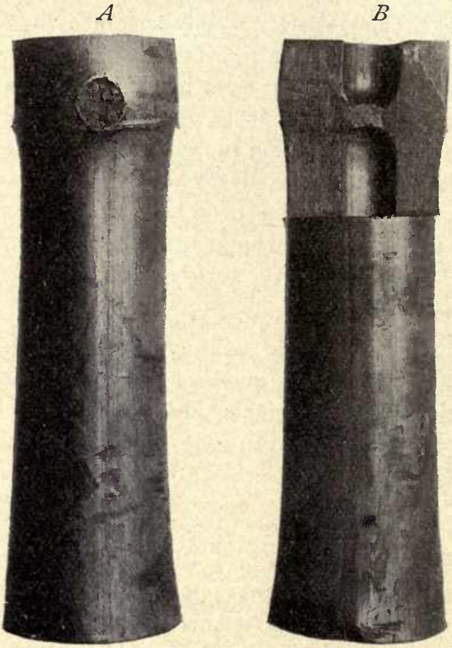


FIG. 107.
Stem of Bamboo including one node at its upper end. In *A* it is seen from outside, with transverse scar of the leaf-insertion, and the circular scar of its axillary branch. In *B* it is cut so as to show the hollow, and the septum which gives added strength. (Reduced to ½.)

from "buckling." On a smaller scale this construction is found also in the stems of pithed Rushes and Sedges, and in many herbaceous Dicotyledons. It is only a step from such arrangements to that seen in the Bamboo, or on a smaller scale in the haulm of Grasses; and in some Dicotyledons, such as the Umbelliferae. Here the thin-walled pith present in the young state breaks away, leaving a central cavity surrounded by a cylinder of firmer tissue. In this case the comparison is with the hollow column so largely used in metal construction by man. But it is liable to "buckle," as has been found in the masts and spars of racing yachts, in which internal ties of metal have been used to meet that risk. In the haulms of Grasses, and conspicuously in the large Bamboos, hard woody septa at the level of the leaf-insertions serve the same purpose (Fig. 107). Without these it would not be possible for hollow stems to uphold the huge head of leaves one hundred feet above ground against all winds, as the Giant Bamboos do.

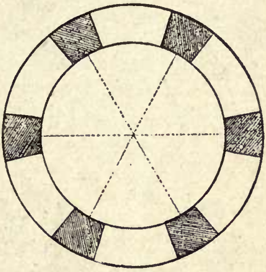


FIG. 108.
Diagram of crossed girders. See Text.

The hollow cylindrical stem of a Bamboo, or of a straw of wheat, may be imagined as corresponding to a series of crossed girders (Fig. 108), with the straps or flanges all fused laterally, so as to form a firm peripheral band. The effective material is placed as far as possible from the centre. The straps being fused laterally, the connecting plate or web of the individual girders can be dispensed with, and the stem is accordingly hollow. But in many cases, and especially in young stems of Dicotyledons, the relation of the

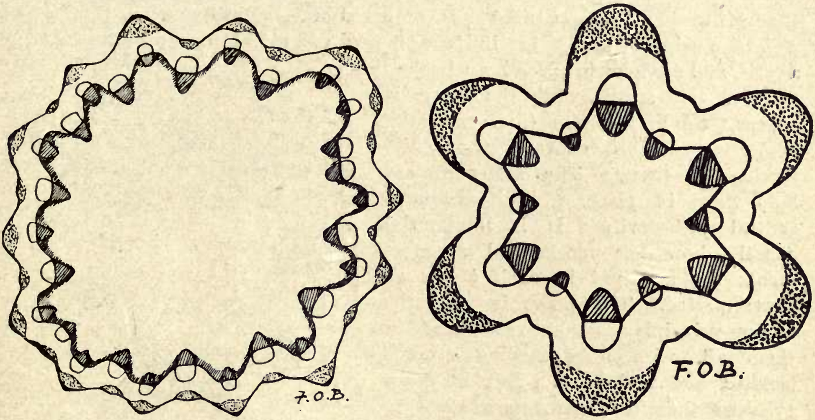


FIG. 109.

Flowering stem of *Astrantia* in transverse section. (× 10.) The collenchyma is dotted.

Transverse section of an internode of a stem of *Clematis*, showing a ring of six larger and six smaller vascular strands, surrounding the central pith, and covered externally by the thick cortex, with six projecting bands of collenchyma. (× 15.)

structure to girder-construction is more plainly seen, since in them the straps of mechanical tissue are not fused laterally. This gives reality to the conception. Thus, in the stem of *Astrantia*, or more clearly in *Clematis* or *Lamium*, the bands of mechanical tissue are isolated, and alternate with softer tissues which keep them in their position (Figs. 109). In *Astrantia*, the resolution of the whole arrangement into a girder-construction is less obvious because of the large number of the strands, and their slight irregularities ; and this is common in herbaceous Dicotyledons. But in the case of *Clematis* only three crossed girders enter into the construction, so that the method appears clearer : and still more so in *Lamium*, where there are only two. There are other points of wide application illustrated in these cases. The stems are fluted, with projecting angles, and one strap of mechanical tissue is seated in each. This gives added strength on the principle of the fluted column, the depth of each girder being thereby increased. The second point is that one of the stronger vascular strands is opposite each of the mechanically strengthened ridges, so that the construction of the stem, as it grows older and the vascular strands become mechanically more effective, resembles that of a number of peripheral girders disposed in a ring. This method is seen in the frames supporting large gasometers.

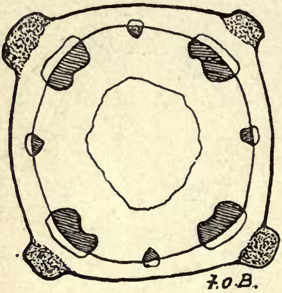


FIG. 110.

Transverse section of stem of *Lamium*, showing projecting angles of collenchyma (dotted), opposite four larger vascular strands: an arrangement equivalent to two crossed girders. (× 14.)

The central tissue may even be replaced by a cavity filled with air, which gives added point to the comparison. The simpler construction of the stem in *Lamium* may be compared mechanically with that of a lattice signal post. In it four bands of metal occupy the four angles, and are kept in place by a latticework of thin straps, while the centre is hollow. So in *Lamium* (Fig. 110), the projecting angles contain the chief mechanical tissue The softer tissues hold them in place, while there is a central pith-cavity It is immaterial exactly how the mechanical arrangements are analysed in such stems as these quoted. The point is that the girder principle can be recognised in them all, with strengthening strands isolated and peripheral. But in Dicotyledons these arrangements are apt to be lost sight of as the stems grow older, owing to secondary thickening, and the development of the vascular ring into the central column of wood (p. 46, etc.). The stem thus assumes at last the type of the solid column. In large tropical trees a further mechanical device is often seen at the base. By unequal thickening broad flanges are produced, which radiate outwards, and act in support like the buttresses of a Gothic tower. The final result of such development might be compared with the outline of the greatly widened base of the Eiffel Tower.

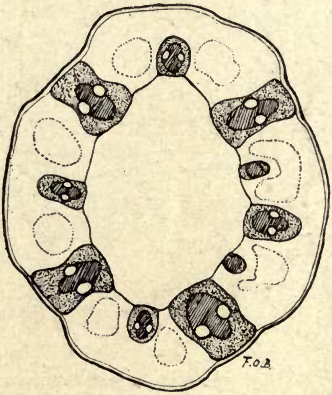


FIG. 111.

Transverse section of the shaft of *Scirpus* (*Eleocharis*) *caespitosus*, showing four large girders, with smaller and less perfect girders between them. Centrally is a large cavity. The dotted areas indicate thin-walled water-storage tissue. (× 62.)

Similar principles hold also for the stems of Monocotyledons; but the circumstance that their closed vascular strands are usually scattered over the transverse section tends to complicate their scheme of construction (p. 44). On the other hand the absence of cambial thickening makes its recognition in the mature stem easier. Commonly the sclerotic tissue accompanies each vascular strand, as bands following its course, or even as a sheath encircling it (Fig. 32). Such an arrangement is in itself comparable with a girder, and occasionally, where there is a ring of vascular strands thus invested, the construction is simply a circle of sub-epidermal girders, as in *Scirpus* (*Eleocharis*) *caespitosus* (Fig. 111). Sometimes the sclerotic bands may be quite separate from the

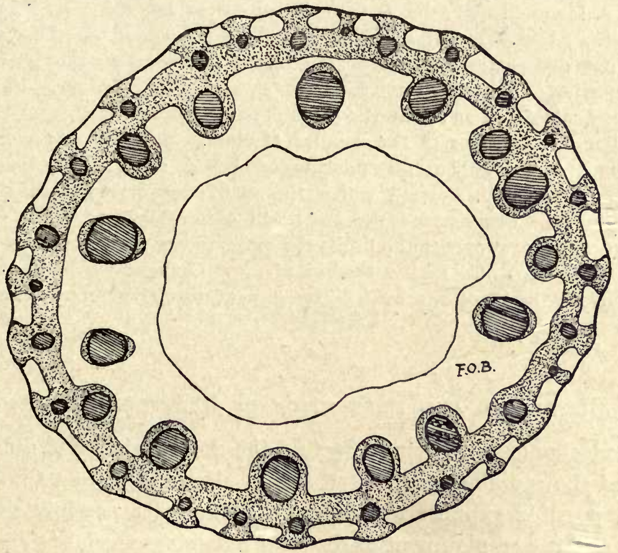


FIG. 112.

Transverse section of the flowering shaft of *Molinia coerulea*. Centrally is a large cavity. Thin-walled tissue is left clear: sclerotic tissue is dotted, vascular strands cross-hatched. The peripheral vascular strands are embedded in a continuous ring of mechanical tissue. (× 40.)

vascular strands, though usually opposite to the strongest of them, as in *Schoenus nigricans* (compare Fig. 29, p. 44). These simple arrangements are very like those seen in the Dicotyledons. But in most Monocotyledons the vascular strands are scattered over the transverse section, and this introduces a good deal of variety of detail. Where the vascular strands are thus scattered, and the mechanical construction more complicated, the sclerotic bands may be fused together laterally in various ways. A continuous sclerotic ring may thus be formed, and the vascular strands be embedded in it, with or without flanges projecting from it (Fig. 112). Such structure developed on a larger scale, and with more general fusion of the sclerotic tissues, leads to the condition seen in the large Bamboos and Palms.

The case of *Molinia coerulea* proves how effective this mechanical strengthening actually is. The structure of the haulm is shown in transverse section in Fig. 112. At its base it is about $\frac{1}{16}$ of an inch in diameter, but it is there supported in some degree by its sheathing leaves. It may grow in favourable cases to a length of 30 inches before bearing its inflorescence. Thus the length of the stem is to its diameter as about 500 to 1, and still it can uphold the inflorescence at its distal end, together with the weight of the fruit when ripe. This extreme proportion of length to diameter suffices for a small Grass; but it cannot be maintained indefinitely for larger structures. For the weight of a structure varies as the cube of its dimensions, while the strength varies only as the square. There must be then a limit of size beyond which it becomes impossible for a certain type of structure to maintain its form. For instance, according to the proportion of the *Molinia* stem, a ten-foot fishing rod should only be ¼ inch in diameter at the butt; but it is thicker than that. A striking case is seen in the Giant Bamboos. Ewart quotes one 60 metres high, and 40 cms. in diameter at the base. That is a proportion of only about 150 to 1. For a plant of that size these dimensions have been calculated as about the limit possible, though the proportions are less striking than those of the smaller *Molinia*. There is in point of fact a size-limit for any plan of construction based upon a certain quality and use of material, beyond which the plant cannot maintain its form. If this limit be overstepped the stem will either bend or break. In the Bamboo, which approaches the limit, the extreme top does bend in a graceful curve; as it does also in the haulms of most Grasses, which like *Molinia* approach the limit of mechanical resistance resulting from their actual dimensions and structure.

(*b*) Stiffening and Protection of Flattened Surfaces.

The mechanical problems affecting the dorsiventral leaf differ from those of the radially constructed stem. The end to be gained is the largest possible expanse of blade, with the least possible risk from winds, and the employment of the least possible material. The elastic petiole allows the blade as a whole to yield before the wind. In the extreme case of the Aspen, where the least breath causes a shiver of the leaves, the petiole is laterally compressed so as to be very flexible. But in most leaves it is stiffer, and semilunar in section, with the convex side downwards, an arrangement which secures efficient support for the blade, while still permitting some freedom of movement. (Fig. 42, p. 59) Another feature of mechanical importance is the cutting of the larger leaves into segments, so that while the aggregate area may still be considerable, no unduly large surface is exposed to the wind. The risks of a large leaf-area are two: first, that of folding into so sharp a curve as to crush the soft mesophyll between the firmer layers of epidermis; and second, that of tearing from the margin inwards. The former is met by the vascular venation, which is often accompanied by sclerotic strands, and by enlargement of the surrounding tissues so as to form strong ribs. The latter danger is met by arched venation, which is often aided by marginal deposits of sclerenchyma. The whole blade is held together by the upper and lower layers of epidermis,

A

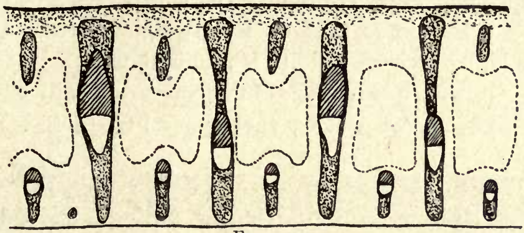


FIG. 113.

B

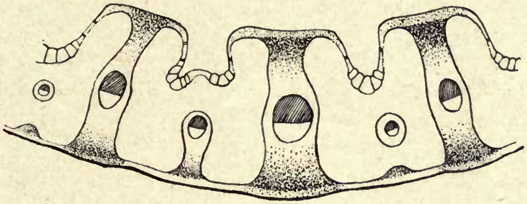


FIG. 114.

C

FIG. 115.

FIG. 113. *A*, Transverse section of the leaf of *Phormium tenax*, New Zealand Flax. FIG. 114. *B*, ditto, *Elymus arenarius*. FIG. 115. *C*, ditto, *Deschampsia caespitosa*. (× 20.) Thin-walled tissue left clear: mechanical tissue dotted; xylem cross-hatched. Aqueous cells in *B* and *C* indicated diagrammatically. In *A*, aqueous areas are outlined with dots. The involutions in *B* and *C* appear in positions opposite to the aqueous areas in *A*. (F.O.B.)

which, having a thickened outer wall, form a firm skin over the softer mesophyll within. Sometimes the mesophyll may be itself sclerotic in places, as it is in many Monocotyledons.

The structural stiffening of the flattened blade against folding is best illustrated in the leaves of Monocotyledons, for there the parallel venation makes the transverse section appear simpler. All the main veins are then cut at right-angles, and in simple cases each may present an appearance as in Fig. 106, p. 148, of *Cyperus*. Sclerotic strands follow the veins on either side, forming with each a girder, as above explained. Since these girders run parallel, and are held in place by the firm upper and lower epidermis, the construction of the whole is on the same principle as that of a lattice-girder railway-bridge, in which also a high degree of rigidity is required, together with economy of material. In some, as in the old Charing Cross railway-bridge, the tracks run between the girders, that space being left vacant in the

FIG. 116.
Photograph of the skeleton of a Dicotyledon leaf, showing reticulation with successive intra-marginal arches. (Natural size.)

construction. In many leaves of Monocotyledons the corresponding space between the girders is occupied by mechanically ineffective mesophyll, while in some there are large thin-walled cells for water-storage (Fig. 113). It thus appears that the requisite stiffness of Monocotyledon-leaves is gained by means very similar to those employed by engineers to obtain like results in bridges. But irregularities are frequent, especially in thick leaves. The girders may be incomplete, or the sclerotic bands may be fused laterally. But still the girder-principle may be recognised as underlying such deviations.

The most interesting variants are those seen in xerophilous grass-leaves, which curl automatically so as to check transpiration. Native examples are seen in the Sheep's Fescue, the Marram, Lyme, and Tussock Grasses (Figs. 114 115.) Their mechanism shows a reduction of the mesophyll with a corresponding involution of the surface between the girders, while the latter are specially deep. The upper leaf-surface is thus marked by parallel grooves, the aqueous cells at the bottom of each furrow being large and thin-walled. The lower side of the leaf is sclerotic, so as to maintain its outline, while the upper is liable to shrink with drought. Such shrinkage draws the margins together. The sloping faces of the grooves, which bear the stomata meet, and transpiration is checked. Access of water, on the other hand, swells the aqueous cells, and the leaf flattens out again.

The Monocotyledon leaf, with its parallel venation is usually secure from marginal tearing. A prominent exception is seen in the Banana, where the huge leaf seldom appears perfect in plants grown in the open. It has a midrib from which the veins run out parallel towards the margin, on the plan of a feather. These leaves are readily slit to ribbons by the wind, from the margin inwards, since there is no sufficient marginal protection. In most Palms a similar subdivision of the leaf is carried out during development, by the plants themselves. Certain tissue-tracts dry up, cutting the blade into segments, and giving the appearance when mature of a true pinnation. For smaller leaves tearing from the margin is still a risk, and there are structural arrangements which prevent it. The commonest is the curving of the veins into intra-marginal arches (Fig. 116). Several series of these of successively smaller size towards the margin, effectually check tearing. The most dangerous spots are naturally the indentations in toothed or deeply cut leaves. These are often protected by small "gussets" of indurated tissue at the base of each sinus. Good examples are seen in Ferns, as in the genus *Asplenium* (Fig. 117); or a special strongly arched vein may run across the point of deepest indentation; while not uncommonly a patch of sclerotic cells may be fused with it at the point of danger (Fig. 118). This is often continued along the margin as a sclerotic band, which serves, like the hem of a handkerchief, to prevent a marginal tearing. Similar hems are found in many ordinary leaves, but conspicuously in xerophilous plants. Good examples are seen in the Date Palm, and in the Gum Trees. The

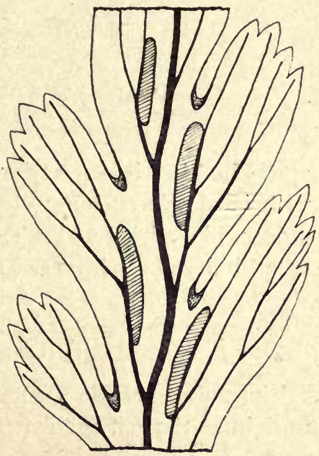


FIG. 117.
Part of leaf of *Asplenium horridum*, showing "gussets" dotted, at the base of indentations. (Slightly enlarged.) F. O. B.

marginal stiffening becomes actually aggressive in spinous leaves, such as the Holly, Barberry, and Gorse. A particular instance of a like sclerotic development that serves a peaceful end is seen in the Sand Sedge. It burrows with its creeping rhizome through the sand. The

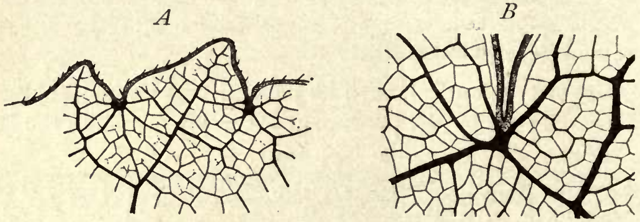


FIG. 118.
"Gussets" at margins of the indentations of leaves (*A*) of the Elm, (*B*) of the Sycamore, showing their relation to the vascular network, and to the mechanically strengthened margin. (× 14.) F. O. B.

apical bud has its successive scale-leaves developed to a point, tipped with hard sclerenchyma, by means of which it passes through soft objects like a brad-awl. These are a few examples of the mechanical adaptibility of the leaves of Flowering Plants.

(*c*) THE ROPE-REQUIREMENT.

Those parts of the plant, such as roots or rhizomes, which hold it upright in the soil against the impact of winds are subject to longitudinal tension, as on a rope or string. In cordage, in order to resist such tension, the fibres are twisted together so as to be grouped in as small a transverse area as possible. This method secures the even distribution of the strain over them all. A similar condensation of the mechanical tissues, but without the twisting, is usual in roots. Their stele is small compared with the whole transverse section, and it is frequently pithless. But often the xylem stops short of the centre, which is then occupied by sclerotic tissue. This links up the xylem, so as to form with it a resistant central cord (compare Fig 73, of *Acorus*). In larger roots a pith may be present, surrounded by a dense ring of mechanically effective tissue composed in the same way (Fig. 119). But still the

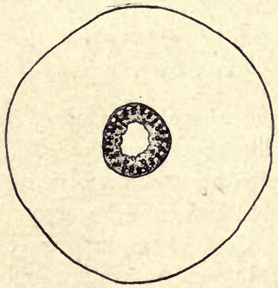


FIG. 119.
Transverse section of root of *Ruscus* showing large proportion of cortex to the contracted and pithed stele. (× 12.) F. O. B.

stele is compact as compared with that of the axis. Underground rhizomes show a similar construction. Their stele is contracted, and their cortex widened, as is seen in the Marram Grass, and still more clearly in the Sand Sedge, where the cortex is very weak and

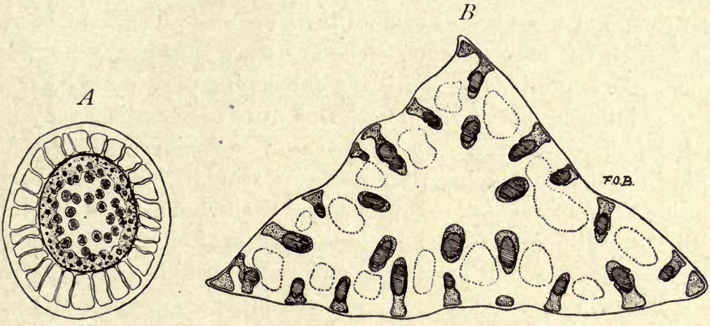


FIG. 120.

Sections of stems of two Sedges. *A*, Rhizome of *Carex arenaria* with mechanical tissue condensed centrally, as resistant to the rope-requirement. (× 14.) *B*, *Carex vulgaris*, aerial stem constructed to meet the columnar requirement. (× 25.)

lacunar, while the stele is compactly cemented together with sclerotic tissue, so as to form a solid core (Fig. 120, *A*). This is in sharp contrast to the aerial stems of most Sedges (Fig. 120, *B*). Stems supporting heavy, pendent fruits show a like structure; also submerged and some climbing stems, all of which are liable to longitudinal tension. The similar modification of plants of such various habit, when subjected to the same mechanical demand, indicates that the rope-like concentration is adaptive.

The problem for strut-roots, such as are seen at the base of the stem of the Maize, is a mixed one; for the roots on the windward side of the plant suffer longitudinal tension, while those on the lee side act as oblique struts, and are subject to columnar pressure. The structural requirements are thus opposed. The mechanical tissues in such roots are found to form two systems (Fig. 121). The stele is compact, and cemented together in a hollow ring, which is, however, wider than in the underground roots. It is suited to resist longitudinal tension, but is not highly specialised to meet it. The cortex is, however, sclerotic, the thickening being greatest at the periphery. This is suited to meet the columnar

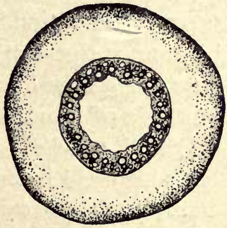


FIG. 121.

Transverse section of strut-root of *Zea Mais*. The mechanical tissue of the cortex is dotted. (× 12.) F. O. B.

requirement. Thus the mixed problem is solved by a structure that serves both purposes.

Such cases as those quoted in the last paragraphs confirm the view which follows inevitably from the study of the distribution of the mechanical tissues generally in plants, viz. that those methods are adaptive, and have been acquired in the course of Descent in accordance with the requirements. The structure is as a rule hereditary, though the conditions to which the developing part are exposed may have an influence in determining the quantity of sclerotic tissue formed in the individual part. There is reason to believe that the forces acting on the developing part serve as stimuli, increasing or even causing the formation of the mechanical tissue. This is in accordance with the well known fact that those tendrils of climbers which grasp a support develop much more strongly, and are able to bear a greater load than those which do not. In the large woody climbers of the tropics the difference is often very marked, the fixed tendril developing as a large woody structure.

While such observations are in themselves interesting in their bearing on the quantity of the mechanical tissue present, they do not explain the origin of the methods of its distribution. The degree of parallelism which those methods show to the methods of modern engineers in using their stone, steel, and concrete, is remarkable. While we admire the efficiency of the result in either case, and especially the economy of material made possible by such methods, it is to be borne in mind that undoubtedly the priority of initiative lies with the Plant. For many of the methods represented by ancient types of vegetation have only been adopted within the last few decades by man. Nor is there evidence that engineers ever took, as well they might have done, any suggestion from the study of the engineering methods of Plants. What we see in the two cases is accordingly a result of *parallel, or homoplastic development.* Similar results have been acquired independently along two quite distinct lines of evolution. In the one case the results have followed from human calculation and experiment, in the other they are described as "adaptive." But it is still an open question in what degree the structures seen in plants, and so designated, are causally related to the requirements which they so effectively meet.

CHAPTER X

MODIFICATIONS OF FORM IN THE VEGETATIVE SYSTEM

It has been seen that the primary construction of the Higher Plants is according to a general and uniform plan (p. 15). But the scheme may be worked out in detail in very different ways. Either the root or the shoot, or both, may vary in form and proportion in different plants. Such differences are clearly related to the conditions under which the plants grow. Since it is possible in very many cases to see that the particular form taken is suitable for successful life under corresponding particular conditions, such forms are described as being *specialised*, or *adapted* to them. The special modifications of form which lead to success are described as *adaptations*, and will be so grouped here: though with the same reservation as to causality as that expressed at the close of the preceding chapter, with reference to internal structure.

Plants may be recognised as being thus adapted to the *medium* in which they grow; as for instance, in water or in air: to other *physical conditions*, such as the action of gravity, or the direction of light: to the *climate* to which they are exposed, hot or cold, dry or moist, equable or with marked seasons, quiescent or stormy: or to the *soil* which provides them with requisite supplies: or they may show special features which enable them to take advantage of other surrounding circumstances. Prominent examples of this are seen in plants which *straggle* or *climb* over others; or in those which, by taking to some irregular form of nutrition, derive advantage from their neighbours as *parasites*, or in other ways. A few examples will be taken illustrating this adaptability of the plant; but it would be impossible in the present work to treat so wide a subject exhaustively. It must suffice to refer for this to the *Natural History of Plants*, by Kerner and Oliver (Blackie & Son, 1895, 4 vols.); or for the consequences of adaptation as shown in the distribution of British Plants to *Types of British Vegetation*, by Tansley (Camb. Univ. Press).

Biology of Season and of Duration.

If we attempt to sketch a general, that is a non-specialised type of Flowering Plant, it would have a cylindrical upright stem, bearing leaves with petiole and lamina radiating out on all sides of it, and with axillary branches repeating the characters of the main shoot. Its root-system would consist of a tap-root and lateral roots of successive orders, all fibrous. A young Sycamore or Apple-tree would answer this general description. Further, it seems probable that the perennial state was prevalent, or even constant among early Vascular Plants. For it is seen almost exclusively in living Pteridophytes and Gymnosperms, and it is characteristic of the early fossils. So that in this respect, as also in their general form, an Apple or a Sycamore may be held as representing a type of vegetative construction usual for early Flowering Plants.

In one marked feature, however, the Sycamore and the Apple are certainly adaptive. Both are *deciduous*, that is they drop their leaves in autumn, as do most of our British trees and shrubs. *Leaf-fall* is clearly related to season. It brings the biological advantage of reducing the transpiring area at the time of low temperature, when the activity of the roots in the cold soil declines. It is in fact a provision against what may be called *physiological drought*, for the roots in the cold soil in winter are unable to make up for any great loss of water by transpiration. But many familiar plants retain their leaves during the winter, as "evergreens." They are mostly shrubs with leathery leaves, and many of them have been introduced from southern lands, such as the Rhododendron and Cherry-Laurel, from the Levant; but Holly, and Yew, and Ivy are native evergreens.

The evergreen state is more common in plants of lands where the seasons are equable, and it is probably a primitive state, while the deciduous habit has been acquired in species that have spread to regions with marked seasons. On the other hand, in hotter climates than our own, a dry and hot season may also be tided over by many plants by a fall of their leaves, and a new suit of leaves is usually formed after the commencement of the rains. The physiological explanation is similar to that of our autumn leaf-fall at home. It is a protection against drought. But the drought thus met in the tropics is a real lack of water in hot weather. In very hot dry seasons our own trees sometimes drop their leaves in the same way. Thus by a simple modification plants can limit their transpiring area temporarily. However prominent the fall of the leaf in autumn may appear to be, it is not a fundamental feature, but only a special adaptation to season.

The annual habit may similarly be regarded as an accommodation to seasonal change. The seed is more resistant to extremes of temperature and drought than the growing plant. If then the vegetative development, from germination to flowering and fruiting, can all be completed within one growing season, an adverse period can be safely passed as seed, and the species will survive. Practically this has proved more effective in temperate than in tropical climates, as is shown by the prevalence of annuals in the temperate Flora. On the other hand, annuals are few in forest areas, which are less favourable to their growth than open ground. In particular the Arctic and Alpine Floras consist almost entirely of perennials. This is easily understood, since the vegetative season is there too short for the completion both of vegetation and propagation. The fact is illustrated by the Alpine Flora of the Scottish Hills, which is distinctively Arctic in its character.

Perennation and Storage.

Perennation, that is the maintenance of the individual from year to year, presents no difficulties where the seasons are equable, as in many tropical areas, where perennials, growing steadily on from year to year, form the chief element in the Flora. But in temperate regions, with their strongly marked seasons, various adaptations of the vegetative shoot besides that of leaf-fall may be seen, especially in herbaceous plants, for tiding over the winter. They are mostly associated with the *storage of material*, which is thus carried over from one season to the next. The simplest case is that of biennial plants, such as the Evening Primrose and Foxglove ; or, among cultivated plants, the Turnip, Carrot, Beet-root, or Onion. These in their first year store their surplus nutriment in the vegetative organs at the base of the plant, and use it up in flowering and fruiting in the following year, after which the plant dies. Extreme cases of this method, where the vegetative period may extend over several years, and is terminated by flowering, fruiting, and death of the individual, are seen in certain Bamboos, in *Agave*, and conspicuously in the large Palm, *Corypha*. This plant, after years of vegetative growth, flowers with an inflorescence thirty or forty feet in height, fruits profusely, and dies.

On the other hand, if the flowering be not profuse the perennation may go on indefinitely, as in ordinary bulbs and herbaceous plants. Each year a surplus of food-material is laid aside in underground parts. In the autumn the aerial parts die away, but the stock remains dormant and usually buried underground. Its store is thus protected from the rigours of winter, till in spring fresh shoots develop similar to those of the previous year. Most of these plants form their leaves first, and they have the advantage of developing more rapidly than in germination, as they can draw on the store already in hand. But some flower at once, even before their vegetative leaves are fully formed, as in the Christmas Rose (*Helleborus*), the Crocus, and Snowdrop.

For the disposal of their store a slight distension of the tissues is often sufficient in these herbaceous perennials. This is seen in the

FIG. 122.
Perennial stock of *Iris*. *a*, *b*, *c*, successive yearly growths. (After Figuier.)

Iris (Fig. 122), where the short stock grows onwards from year to year, bearing fresh leaves each season and axillary buds, and storing each year's surplus in the massive stem. In other cases the various parts may be considerably changed in their proportions. Thus the roots of the *Dahlia* are swollen to hold inulin (Fig. 123), and root-storage is also seen in the native Orchids, in *Ranunculus Ficaria*, and in *Spiraea filipendula*. But it is more frequently the stem, or rhizome as it is called when underground, that is distended for storage. The familiar corm of the *Crocus* is simply an abbreviated upright stem, a given length of which is swollen for storage in each successive year. That of the previous year is depleted in each spring by the terminal flower, and an axillary bud is distended as the season advances, so as to provide for the next season's growth (Fig. 124). The membranous bases of its withered leaves cover the corm externally, while their axillary buds may provide additional corms. Thus it is an upright branched storage axis, with abbreviated growth. Similar distended axes

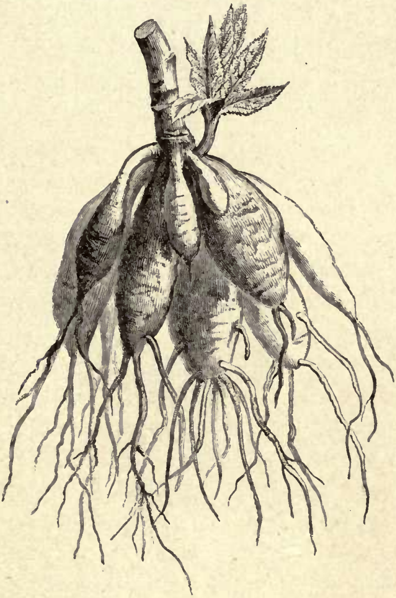


FIG. 123.
Tuberous roots of the Dahlia. (After Figuier.)

FIG. 124.
Corm, or storage stem of *Crocus*. (After Figuier.)

are found in many other perennials, *e.g.* the Tuberous Buttercup (*Ranunculus bulbosus*), and the Pig-Nut (*Conopodium denudatum*). In other cases the storage is in lateral branches borne in large numbers, as in the Potato and Jerusalem Artichoke. These will be considered later in relation to vegetative propagation, to which such developments readily lead. The bulb, as in the Hyacinth, Snowdrop, or Lily, is similarly an upright, abbreviated, perennial shoot, with its growth interrupted by dormant periods. Its biology corresponds to that of the corm; but here the chief storage region is not the axis, which remains small and broadly conical, but the bases of the leaves. The whole bulb is in fact a perennating bud, the apex of which terminates in a flower, or inflorescence, while the growth is then continued by one or more leafy buds formed in the axils of the storage leaves (Fig. 125). The plants quoted are sufficiently distinct from one another to show that they are all cases of independent adaptation, though the method of their perennation is the same in each.

Such arrangements are biologically suited to life under strongly marked seasons. The plant starts the active season of each year with a

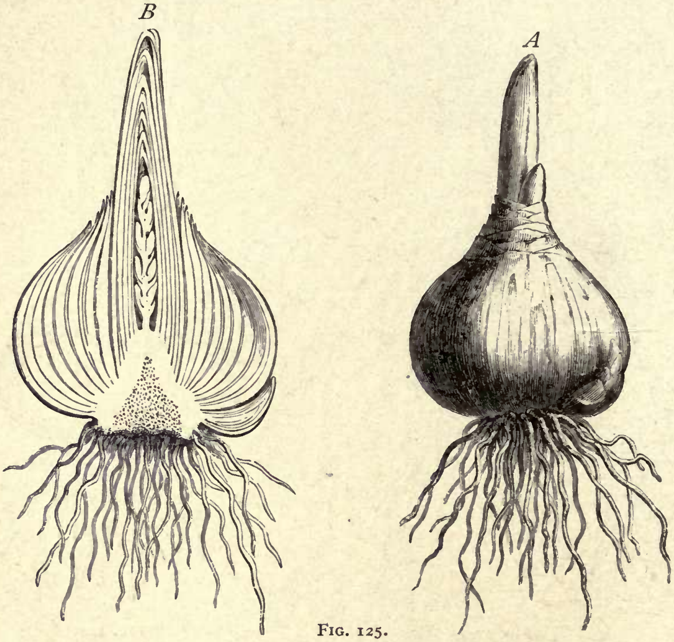


FIG. 125.
Bulb of the Hyacinth. *A*, seen externally; *B*, in median section. (After Figuier.)

sufficient store of nutrition already in hand to support rapid flowering. In the remainder of the active season the store for the next year is acquired by the expanded foliage leaves, and laid aside in the ripening bulb. The bulb-dealer is understood to sell fully ripened bulbs: flower-buds are already present in them, and only wait to expand. The purchaser simply offers the conditions for active growth, and for the transfer of the store to the flowering region. But to ensure a repetition of the flowering in the next year he must fully ripen the bulb again as before. This is often difficult, or impossible in the case of room-culture, or in towns. Hence the dealer has a safe and continued market, based on the ignorance, or the lack of opportunity of the public. The professional bulb-grower secures normal perennation, with seasonal flowering; the purchaser is apt to forget that its continued success depends on nutrition being maintained till the green leaves shrivel, and functional activity ceases for the year. This dormant state, in which the bulb or corm is bought, is itself an accommodation to seasonal drought. The bulb-habit is widely spread, but it is specially characteristic of countries like Southern Europe and the Cape, with a moist spring, but a dry and hot summer.

Symmetry, and its Modifications.

The Root-System, developing in the soil, finds a medium in which the conditions of temperature and moisture are relatively constant; but its form is liable to be strongly influenced by the texture of the soil. Growing roots yield readily to the mechanical resistance thus offered by any large obstacle. But if the roots develop in water, or if the texture of the soil be fine and uniform, as it is in prepared garden soil, the root-system develops with a regular symmetry. When, as in Dicotyledons, there is a definite tap-root, this grows vertically downwards, and the lateral roots radiate from it equally in all directions. Except for the effects of mechanical resistance, the root-system of ordinary plants shows little departure from this regular symmetry, while the individual root is typically cylindrical. It is different where, as in epiphytes, the roots are aerial. Thus those Orchids, which normally grow perched on the branches of trees, but are cultivated in hanging baskets or on cork, often have roots of a flattened form, which follow closely the surface to which they become attached. Occasionally they may even become green, and act as effective organs of Photo-Synthesis. But these are exceptional cases. Speaking generally the root of Flowering Plants retains its uniform cylindrical outline, and the whole *root-system* is built up as *regularly or radially symmetrical.* This fact may rightly be related to the uniformity of its usual surroundings.

The Shoot, on the other hand, is exposed to much more varied conditions than the root. It may be developed in water, still or moving; or if developed in air, it may be subjected to various degrees of lighting and moisture, and to winds from any quarter, as well as to the various incidence of gravity. It is possible to trace, in the different forms of the shoot which we see, a relation to and fitness for its surroundings. It would be strange if the shoot, which is so adaptable individually as we have seen it to be (Chapter VIII.), should not show variety of conformation in the race, seeing that its surroundings are so various. It may not be possible to correlate all its forms directly, or even indirectly with circumstance. The difficult question of the actual method, by which such adaptive features as we recognise may have been produced in Descent, must also be left aside. But we may agree to accept as results of adaptation those features which harmonise with the surroundings: and from this point of view the shoot and its parts may be studied comparatively.

An ordinary *upright shoot* develops as a rule with *radial symmetry*, that is equally all round the central axis. The axis being cylindrical meets equally the impact of all winds, and its leaves radiate out from it as a centre, occupying a circular area whose radius is the length of the mature leaf. This type is probably a primitive one, and is very general. But it may be worked out variously in detail as regards the arrangement of the leaves, as well as in their form, so as to secure an approximately equal exposure of all the leaves to the incidence of light. It is obviously undesirable that one leaf shall overshadow another, and it is interesting to observe the various ways in which this may be avoided.

FIG. 126.
Transverse section through the apical bud of *Epilobium angustifolium*, L., showing a symmetrical 2 × 2 system. (After Church.)

Following on the paired seed-leaves, the plumular leaves of Dicotyledons are often paired also, and at right angles to the first pair (*decussate arrangement*). This arrangement may be maintained through life, as it is in the Dead-Nettle, Willow-herb (Fig. 126), Lilac, Sycamore, or Horse-Chestnut. The upright shoot of the Sycamore is a good example how the circular area round the axis is put to the best use by leaves arranged on a decussate plan. Each successive pair fits into the gap between those of the preceding pair. But if the internodes were short, as they are in the young state, the higher would overshadow the next pair but one of lower leaves. This difficulty is met by the lower pair having longer petioles, so that their blades are carried out beyond those of the leaves immediately above them, forming a compact "*leaf-mosaic*" (Fig. 127).

The decussate is the simplest of the *cyclic* or *whorled* arrangements, where two or more leaves are seated at the same level. But in other cases the number of the leaves at the same level may be not two only, but three, four, or more. As in the decussate plan the leaves of each succeeding whorl alternate as a rule with those of the preceding, so that they occupy the spaces between them, an arrangement that is very convenient in the packing of the crowded parts into small compass in the bud. A transition to higher numbers in the cycle may be seen in the individual plant. Thus in *Fuchsia*, which has usually decussate leaves, a very strong shoot may bear alternating whorls of three. In *Lysimachia vulgaris*, and in the Privet, a like variability is common. It is styled *meristic variation*, and one factor in producing it is probably the size of the apical cone, which, when

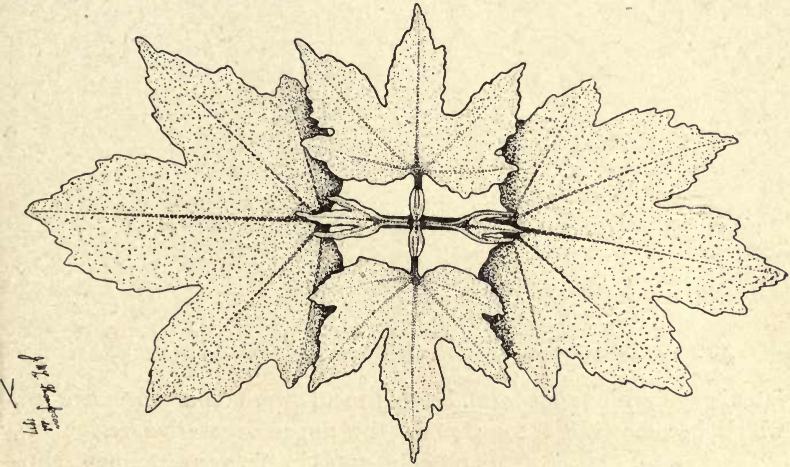


FIG. 127.

Young leafy shoot of sycamore seen from above: showing how with very little overlapping the leaf-blades form a mosaic. The spaces unoccupied centrally will be filled as the younger leaves expand.

large proportionally to the leaf-primordia, can accommodate a larger number of young leaves at the same level. Such variations are common in the floral region, where cyclic arrangements prevail. (Compare Floral Diagrams in Appendix A.)

But in most Dicotyledons, and very generally in Monocotyledons, the arrangement of the leaves is *alternate*; that is, they are seated singly, each at a different level upon the axis. The arrangement is often such that an ascending spiral line may be drawn round the stem so as to thread together the bases of them all. Such arrangements are therefore described as *spiral*. That the cyclic and spiral modes of arrangement are not essentially distinct from one another is shown by the fact that both may appear successively in the same plant. For instance, in the Sunflower, the seedling starts with paired cotyledons, followed by decussate leaves of the plumule (Fig. 127 *bis*, A), which arrangement may be maintained for a time (C); but sooner or

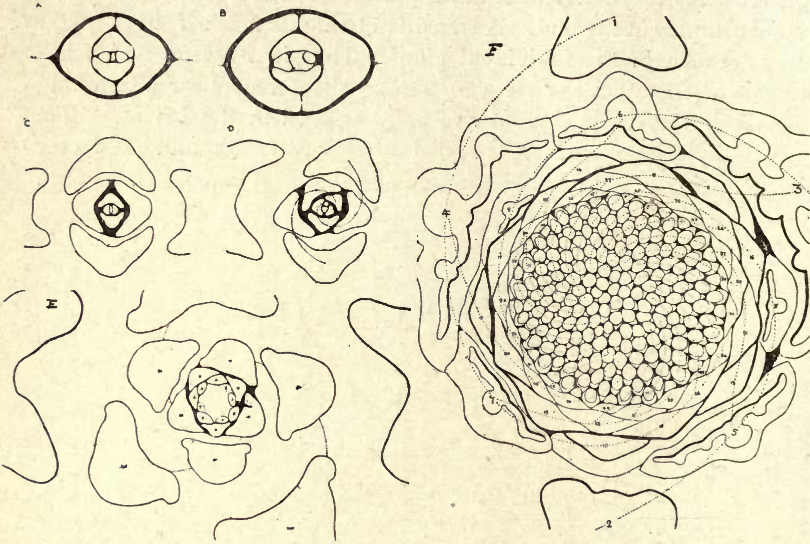


FIG. 127 *bis*.
A-F. Ground-plans of buds of Sunflower of different ages. See Text. (After Church.)

later irregularities appear (B), leading to an alternate arrangement (D), which becomes more complex in the upper vegetative region (E), and culminates in the very complex structure of the flowering head (Fig. 127 *bis*, F). It will be unnecessary for us to trace these successive stages out into detail, though they are found to follow certain definite methods. The point is that from a cyclic beginning a spiral disposition is arrived at. As the individual plant develops and its apex expands, the complexity of the arrangement of its appendages increases. The individual life of the Sunflower illustrates a relation that is usual, viz. that complex spiral arrangements are found where a widened axis develops with short internodes, and where the crowded primordia of leaves are of relatively small size. Such spirals may be seen either in the vegetative or the floral region. A very beautiful example

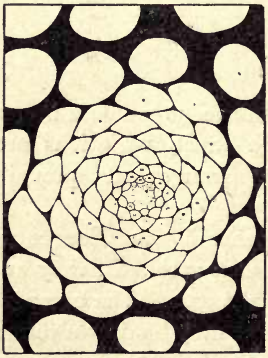


FIG. 128.
Transverse section through bud of *Sedum pruinatum*. (After Church.)

is shown in the vegetative shoot of *Sedum pruinatum* (Fig. 128). A biological consequence is that with very numerous leaves each obtains a maximum of exposure to light incident from above. It is also to be remembered that, as the branching is axillary in the flowering plants, the position of the branches themselves will follow the arrangement of the leaves. This still further defines the external form of the mature organism.

The different types of spiral are designated according to the angle between the median planes of the successive leaves. This is called the *angle of divergence*, and is expressed as a fraction of the complete circle. It is found

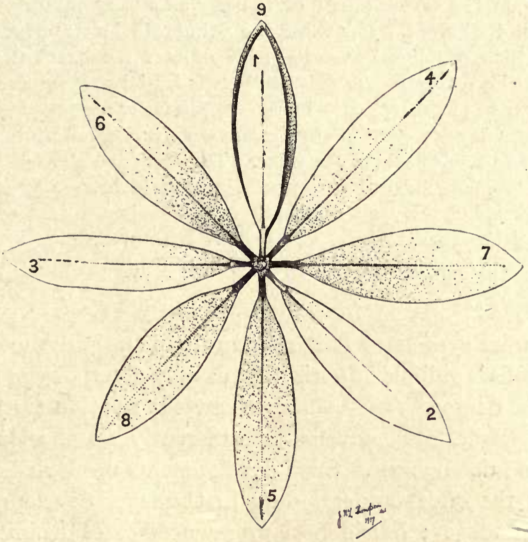


FIG. 129.

Accurate drawing of a shoot of *Rhododendron*, seen from above. The successive leaves are numbered, and it is seen that the ninth is covered by the first, while an imaginary spiral including all their bases successively, will have encircled the stem twice. That is, the angle of divergence between any two successive leaves is $\frac{3}{8}$. (Reduced to $\frac{1}{2}$.)

that in many plants, and even in whole families, certain angles are constant in the mature shoot. This gives a comparative, or even a systematic value to their observation. For example, in the Grasses, and in *Iris*, the angle of divergence is $\frac{1}{2}$, that is, the leaves are alternately on opposite sides of the stem, the third being above the first: they thus constitute two longitudinal rows. In the Sedges, *Veratrum*, and other Monocotyledons the angle is $\frac{1}{3}$, the fourth leaf being above the first, and their arrangement being in three longitudinal rows. In the Rosaceae and many other Dicotyledons a common angle of divergence is $\frac{2}{5}$ths, and the leaves are arranged in five rows. Consequently the sixth leaf will be directly above the first, while the imaginary spiral threading their bases together will have passed twice round the axis before reaching it. Other more complex arrangements are expressed by divergences of $\frac{3}{8}$ (*Rhododendron*) (Fig. 129), and $\frac{5}{13}$ (*Dracaena*), etc. These higher divergences go along with shorter internodes, and compact grouping of the leaves; while their overlapping is avoided by the spiral arrangement.

Though we may recognise the biological advantage of such arrangements, this provides no direct causal explanation. Various theories have been propounded. The old spiral theory assumed an inherent tendency to spiral organisation in plants, and, deductively, attempts were made to read spiral construction into all shoots. Subsequently a theory of contact-pressures was suggested, according to which the spirals resulted from mechanical arrangement of the leaf-primordia upon the axis, comparable to those of marbles in a flat frame. But though such pressures may in certain cases have an effect upon the arrangement of the parts as they mature, they do not explain the initial steps. For when the primordia first appear they are not in contact with one another. In point of fact the exact position of the primordia of leaves upon the axis, and their initial arrangement relative to one another, can at present only be referred to inner causes as yet unknown.

Some plants develop with *bilateral symmetry*, having anterior and posterior, or right and left sides, which are alike. The flattened shoots of the Prickly Pear, or of *Phyllocactus*, are examples, also certain Mosses (*Fissidens*). But the headquarters of this type of symmetry, which is uncommon in Flowering Plants, is in the Marine Algae, and a good example is seen in the common Bladder Wrack (*Fucus*).

Dorsiventrality.

While radial symmetry is thus the rule in upright shoots, those in which the axis is oblique or horizontal usually diverge from the radial in more or less degree. They show an obvious relation to the direction of gravity, light, etc., developing differently on the sides directed upwards and downwards. Such developments are styled *dorsiventral.* Sometimes the effect appears only in the later development of the axes or appendages; but in more pronounced cases the initial arrangement of the leaves is itself dorsiventral.

Examples of the former are seen in the lateral branches of many trees, and conspicuously in many Conifers, such as the Spruce. While the main axis of the "Christmas Tree" is upright and radial, the lateral branches appear flattened. This is due partly to the fact that the lateral branches of higher order have been developed from buds seated right and left on the main branches; partly to the curvature of the leaves upwards. Nevertheless the construction of these dorsiventral branches is essentially radial. If the terminal bud of the main stem be removed, one or more of the lateral buds, which would normally grow into flattened lateral branches, will grow upwards and take its place. With the vertical position, it regains its radial symmetry. Very much the same may be seen in the Sycamore, or the Horse

Chestnut, which retain the radial structure of their leading shoot. Their lateral branches are slightly dorsiventral, but they do not modify the symmetry of the lateral branches so much as the Spruce.

On the other hand, the upright radial shoot, or lead, in many trees may itself become dorsiventral as growth proceeds, while the lateral branches are conspicuously so. Consequently the whole tree when full grown will be made up of flattened shoots, the lateral branches spreading out like fans. (Fig. 129 *bis.*) In the Elm, Beech, and Lime this change of the leading shoot comes early. Their seedlings are radially constructed. In the Elm and Beech the dorsiventral structure, with alternate distichous leaves (in place of the decussate arrangement) appears in the second year of the seedling, and continues from then onwards. But though the whole tree is thus built up of dorsiventral shoots, these may form collectively a radial crown, as in the Elm. Such examples of the transition from radial to dorsiventral symmetry are carried out in each individual plant. They indicate that the radial is the more primitive state, and the dorsiventral derivative.

FIG. 129 *bis*.
Strongly dorsiventral branch of Lime, seen from above. Its leaves form a compact leaf-mosaic. (Reduced to ½.)

In many herbaceous plants the dorsiventral habit is more pronounced than in trees. The whole shoot may take a creeping horizontal position, or a climbing habit by lateral attachment, as in the Ivy. The lopsidedness then becomes marked, and different degrees of it may be noted. Thus in the creeping rhizome of *Carex*, while the leaves show the 1-3rd divergence, the axillary bud in the axil of each fourth downward-directed leaf alone is developed. The apex of the main shoot then turns upwards, while the axillary bud grows on, continuing the false-axis (sympodium). Thus the individual shoot is radially constructed, but the sympodial system is dorsiventral. (Fig. 130.) In other cases the mature shoot may be itself dorsiventral, though that condition is only acquired in the course of the individual development. and is not shown by the apical bud. This is seen in the rhizomes of *Acorus*, where the apical bud shows a bilateral symmetry, with alternate leaves. But in the mature rhizome the two rows are shifted to the upper surface, giving a dorsiventral condition, with roots arising

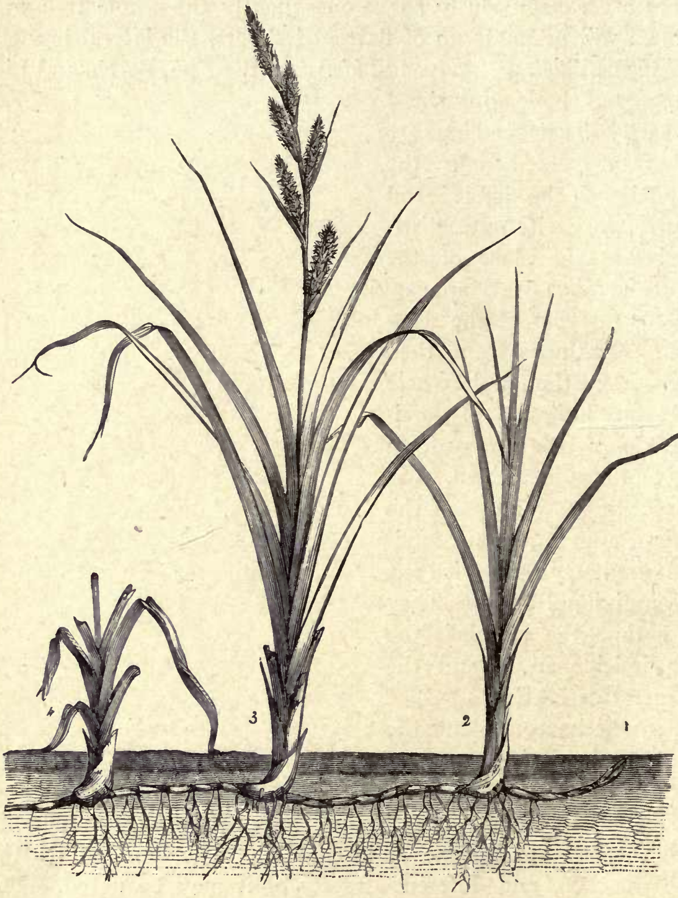


FIG. 130.
Successive sympodial shoots of *Carex*. (After Figuier.)

from the lower surface. In other cases again, and conspicuously in Ferns, the dorsiventrality is fixed already at the growing point, and is not the mere result of any subsequent displacement of parts. This is seen in the Common Polypody, which has from the first distichous leaves placed obliquely on the upper surface of the rhizome, while roots only arise on the lower side. This arrangement is already apparent at the growing point (Fig. 131). Such examples show various steps in the impress of dorsiventrality on the vegetative shoot. Lopsidedness may also appear in the inflorescence of many flowering plants. But, as we shall see later, it is in the Flower itself that it becomes most marked, and of great biological importance. In all cases among the Higher Plants the dorsiventral is probably a condition which has been derivative from the primitive radial state.

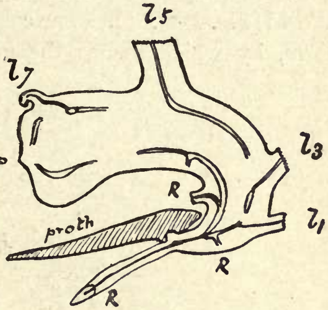


FIG. 131.

Polypodium vulgare. (× 6.) Median section through prothallus and embryo, showing one series only of the distichous leaves l_1, l_3, l_5, l_7. *R*=roots. *ap*=apex of axis. The young shoot becomes inverted, growing backwards over the prothallus.

PLANT COMMUNITIES.

It is thus seen that Climate and other conditions of life are frequently related to special modifications in the plant, which meet special needs. As the conditions will be substantially similar for all plants which grow in a district or specific area, they may collectively take characters which they share in common. Thus they form characteristic *Communities.* The water-relation more than anything else determines such adaptations. Where the climate or conditions are dry, so that water must be carefully conserved, the plants so adapted are termed *Xerophytes.* Where water is abundant, or the vegetation is actually submerged, the plants specially developed under such conditions are termed *Hydrophytes.* Where the water is brackish or salt, plants assume the characters of *Halophytes.* But where the conditions as regards temperature and water-supply are not extreme, though there may be marked seasons, the vegetation would be described as consisting of *Mesophytes.* Such groupings cannot be drawn with definiteness. They must be held as generally descriptive rather than mutually exclusive. In point of fact the communities overlap and graduate one into another. Naturally the distinctive characters impressed upon each community are best illustrated by extreme types.

Xerophyte Vegetation is characterised by various features which have the effect, individually or collectively, of controlling transpiration, and thus making the best of a limited water-supply. The leaf-area is reduced, and its texture is often fleshy, so as to serve for water-storage, as in the Stonecrop, Aloe, or Onion. In other cases leaf-reduction may go along with a corresponding distension of the stem, which becomes green, and takes over the function of Photo-Synthesis. This is seen in the tropical Euphorbias, and Cactaceae, the former especially on the dry areas of the Old, the latter of the New World (Fig. 132). In some cases the stem swells to an almost spherical form, by which means the greatest possible proportion of bulk to

FIG. 132.
Succulent stem and flowers of a Cactus. (After Figuier.)

surface is attained. Succulence with a distended form is thus a frequent character in Xerophytes. With succulence often goes a spinous development, as Fig. 132 shows. It may doubtless be effective as a defence against herbivorous animals. A thorny character is common in Xerophyte vegetation, and is a marked feature in dry districts such as the Veldt of South Africa. Finally, many Xerophytes are very deep-rooted. As special instances of this *Acanthosicyos* and *Welwitschia* of south-west Africa may be quoted.

Along with succulence and reduction of surface go various other structural modifications. In xerophytic plants there is usually a special dermal development, with thickened cuticle. It is often covered with wax, giving a glaucous surface. The stomata may be protected by being sunk in deep pits (Fig. 133).

Additional protection is given in some cases by woolly coverings of hair, as in the Swiss "Edelweiss"; while certain xerophytes bear glandular hairs secreting essential oils, as in Rosemary, Lavender, and many other Labiatae of Southern Europe. Such secretions are believed to be effective as a heat-screen.

A very peculiar specialisation occurs in the Eucalyptus-trees of Australia. Instead of exposing their leaf-surfaces upwards in the usual di-heliotropic way, they hang in a vertical plane, exposing their edges to the zenith. This is brought about by a half-turn of the petiole; but it only appears in Blue-Gum Trees after growth is considerably advanced. In the first leaves the surfaces

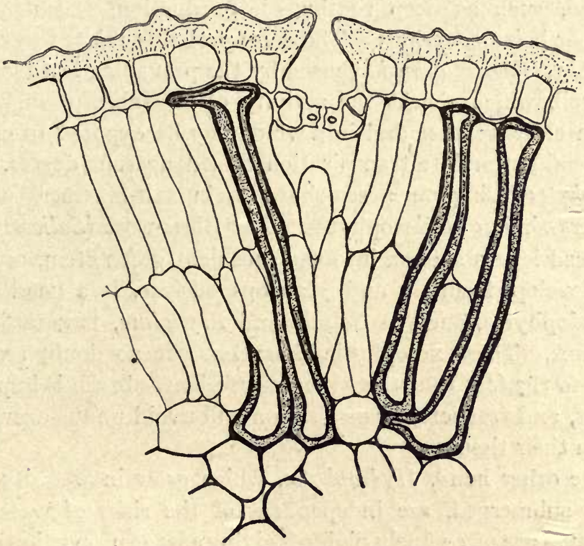


FIG. 133.
Part of a transverse section of the xerophytic leaf of *Hakea*, showing a stoma greatly depressed below the well-developed epidermis, which has greatly thickened outer walls, covered by a thick, continuous cuticle. (× 150.) F. O. B.

face upwards, thus showing the character of the ancestry. By quite different means the same advantage, that of not exposing the leaf-surface to the full blaze of mid-day, is attained by certain Acacias, also largely represented in Australia. In them the petiole itself becomes flattened in a vertical plane, without torsion, while the lamina is abortive. Such leaves are termed *phyllodes*. In the Acacias also the first plumular leaves are often *atavistic*, developing like ordinary Acacia leaves, while the phyllodes usually appear later. Since *Eucalyptus* belongs to the Myrtaceae, and *Acacia* to the Leguminosae—two quite distinct families—these cases give a good example of *homoplasy*, or parallel development, in distinct families of plants under like conditions. Another example of homoplasy has already been seen in the succulent Euphorbias and Cacti. Further instances may easily be multiplied among plants which show special adaptations.

Modifications like those shown by xerophytes are seen also in other plants where water-supply is for other reasons difficult, as it is in those which live attached to the branches or trunks of other plants (*Epiphytes*). Since they have no direct access to the soil, they must receive and store the water from rainfall, or condense it from a moist atmosphere. This is the condition of many tropical Orchids and Bromeliads. In the latter a special surface-protection is afforded by scurfy peltate hairs, while others serve for absorption of water.

Again, in Arctic and Alpine plants many xerophytic characters are presented, such as deep rooting, leaf-reduction, succulence, waxy surface, or hairy coverings. These are probably related to the condition of *physiological drought* caused by the prevailing low temperature of the soil, which checks the activity of root-absorption, while the shoot, in clear weather and in a wind, may be exposed to conditions which would stimulate transpiration to a dangerous degree.

Halophytes living on a sea-shore, or in salt-marshes, also show characters similar to xerophytes. The Glass-wort (*Salicornia*), with its reduced leaves sunken into the succulent green stem, and having a well-developed cuticle and glaucous surface, is a good example. Some halophytes, such as *Salsola* and *Eryngium*, have also spinous protections. These xerophytic characters are no doubt assumed in relation to the fact that the water these plants absorb is impregnated with salt, and restricted transpiration will avoid undue accumulation of salt in their tissues.

On the other hand, *Hydrophytes*, which grow in wet situations or actually submerged, are independent of the risks of water-supply. Their leaves are often finely divided, giving a large proportion of surface to bulk, as in the water Buttercups. They are mostly perennials. The Water-Lily (*Nymphea*) will serve as a good example. Its thick stock is rooted in the mud, and throws up floating leaves with broad lamina and smooth surface. Stomata are absent from the submerged parts, but are present on the exposed upper surface (see p. 63). The shoot contains large air-spaces, with little mechanical or woody tissue. The large air-spaces provide an internal enclosed atmosphere, where gaseous interchange can take place, thus helping to meet the difficulty that diffusion at the surface is slower than is sometimes required. The texture of such plants is limp. Their parts dry up quickly in the air, owing to deficient cuticular protection. These characters, which are common in the Hydrophytes, are in sharp distinction to those of xerophyte types.

The *Mesophyte vegetation* remains to be considered. Excepting in the higher temperature, and the greater intensity of lighting of the latter, the Temperate Zones and the Tropics are alike in presenting conditions very favourable to growth, so long as extremes of season and of water-supply are excluded. In the low lands of the temperate zones and of the tropics, many areas exist where vegetation is easy. Here, when supplied with seed produced by prolific methods, the soil becomes covered with a dense investment of herbage, or of woody plants, in which the potential individuals are more numerous than the ground can carry. Over-population is the character of the sward of any field, as it is habitually of natural woods and forests. Two points emerge from the contemplation of such native or natural growth. One is that plants of very diverse outline and construction may thrive, mixed indiscriminately together. The normal types of Monocotyledons and of Dicotyledons seem to succeed equally well side by side. This indicates that under such conditions there is little need for specialised development. The second is that the overpopulation leads to *competition for space and light.* Evidence of this is found in the commonness of stunted plants, crowded out by the stronger. Any area of densely overgrown ground in a lowland field or wood shows in a convincing way how important access to sunlight really is. The plants engage, in fact, in a race for the light, and the tallest plants win. It is upon this fact that the most striking adaptive feature of the Mesophyte and Tropophyte vegetation is based, viz. the *Climbing Habit.*

The Climbing Habit.

The biological advantage gained by the climbing habit is that the plant which adopts it reaches the light with a minimum expenditure upon its stem. A plant standing alone has to form a strong supporting column. To do this requires a considerable expenditure of material on tissues which are of little physiological use beyond giving mechanical support. If then such support can be attained in some other way, so much material will be gained. That the expenditure is really saved by climbing plants is seen from their anatomy; for their stems show vessels relatively few and large, few other tissues of the wood, and in herbaceous types, though cambium may be present, there is an absence of tissue-masses formed by cambial thickening. There is, however, a well-developed phloem, which in some cases is duplicated on the side next the pith. The vascular strands thus constructed contain little fibrous tissue, and are usually isolated one from another by intervening tracts of soft parenchyma (compare Fig. 25, p. 41).

The result is that climbing stems are relatively weak and flexible, while their leaves, flowers, and fruits may be large. These facts demonstrate their dependence upon attachment to some stronger support.

The *methods of climbing* are various, and they are assumed by representatives of many distinct families ; not uncommonly by isolated species in a genus that does not climb as a rule. But in some families of plants many genera and species are climbers, as in the Leguminosae, Sapindaceae, and Bignoniaceae. The habit is much more frequent in Dicotyledons than in Monocotyledons. Several Ferns have also adopted a very successful climbing habit. This widespread and often isolated occurrence of climbing, as well as the variety of the methods involved, suggests that the habit has been acquired along many distinct lines of Descent. Instances of marked homoplasy are numerous. While climbing is common in our native Flora, it is most frequent here in herbaceous plants, such as Vetches, Convolvulus, or Hop. They may be annuals, like the Black Bindweed ; or perennials with an underground root-stock, like the Hop, or Black and White Bryony. Some few are woody, as the Honeysuckle and Clematis, and Ivy. While this is less common in temperate Floras, it becomes a very marked feature of Tropical Forests. There the huge woody "lianes" develop their leafy shoots far above amid the branches of the lofty canopy of trees, while their flexible but woody stems hang down like ropes, connecting the shoot above with the root-system in the soil. But such climbers of large size do not differ essentially in their methods from the smaller climbers of Temperate zones.

The methods of climbing may be ranged under three heads: (1) *straggling*, (2) *prehensile*, and (3) *adhesive climbing*. The first of these is the least specialised. It is successfully practised at home by Cleavers (*Galium aparine*), and in the south by the Wild Madder (*Rubia peregrina*), herbaceous plants which thread their way through undergrowth or hedge, supporting themselves partly by stiff whorls of leaves expanding at right angles to the axis, partly by hooked prickles borne chiefly on the projecting angles of stem and leaves.

In the Tropics the *straggling method* gives very successful support to larger woody plants. (Fig. 134, i.-vii.) In many cases widely spreading branches in the axils of decussate leaves are an important aid, as in a species of *Lantana*, which was introduced into Ceylon as a decorative plant. It has taken possession of large tracts of abandoned coffee-land, favoured partly by its straggling habit, partly by the spread of its pulpy fruits by birds. The widely spreading branches bear hooked prickles on their projecting angles, which are effective in aiding support. In other cases hooks that aid the straggling are produced from other parts. The climbing Rattan Palms of the genus *Calamus* bear them on the concave side of the whip-like leaf-apices, or of the axillary buds; for it is sometimes the one, sometimes the other, which serves in this genus as the climbing organ (iv.) In the Jujube (*Zizyphus*) there are woody stipules to the leaves which are borne by the curved, whip-like branches. Of these stipules the one that is downwardly-directed of each pair is sharply reflexed, while the other points forwards (ii.). A parallel is seen in *Sageretia,* but in this case it is the axillary buds that are effective, for the lower of each pair forms a recurved hook,

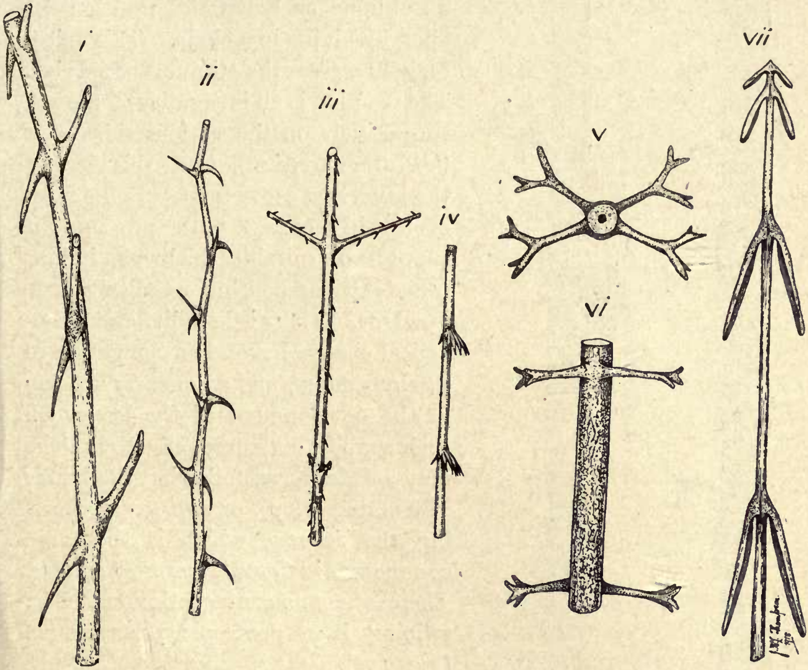


Fig. 134.
Various woody stragglers collected in Ceylon, showing various parts reflexed for support. (i.) axillary shoots of *Sageretia*; (ii.) stipules of *Zizyphus*; (iii.) prickles of *Lantana*; (iv.) prickles of *Calamus*; (v. vi.) axillary branched shoots of *Carissa*; (vii.) reflexed pinnae of *Desmonchus*.

while the upper develops upwards as a leafy shoot. The mechanical effect is exactly the same as in the Jujube, but the parts used are different (i.). In the Palm *Desmonchus,* it is the distal pinnae that are reflexed, and act almost like the flukes of a patent anchor (vii.). A very similar mechanical effect is shown by the reflexed axillary branches of *Carissa* (v. vi.). Such examples illustrate in what varied ways straggling may be made an effective method of support. They involve such diverse parts as emergences, stipules, pinnae, and axillary branches. In fact any part of the shoot-system may be used. The instances come from most diverse families of Dicotyledons and Monocotyledons.

Climbing by *prehensile methods* has gained more attention than straggling, because it is so well represented in the Native Flora, and because the advantages which it brings are so obvious. The attachment to the support may be by a twining stem, as in the Hop, Scarlet Runner, or *Convolvulus*; or by tendrils of various sorts, and by prehensile leaves. The *twining stem* originates from an upright seedling, the tip of which soon takes an oblique or horizontal position, its apex revolving in a circle. This apical region receives the stimulus of gravity. The reaction is an inequality of growth successively on the various sides of it (*lateral geotropism*), and this causes the revolving movement. If the stem comes in contact with an upright support of suitable thickness, it laps round it with a continuous spiral course upwards. There is here little morphological change beyond an elongation of the internodes, and frequently a delay in the development of the leaves till their support is assured. Such climbers may be *dextrorse*, following the hands of a watch (Hop), or *sinistrorse*, showing the reverse, which is the more common, as in *Convolvolus* or *Phaseolus*. There is here no contact stimulus. The twining is a geotropic phenomenon (Fig. 135).

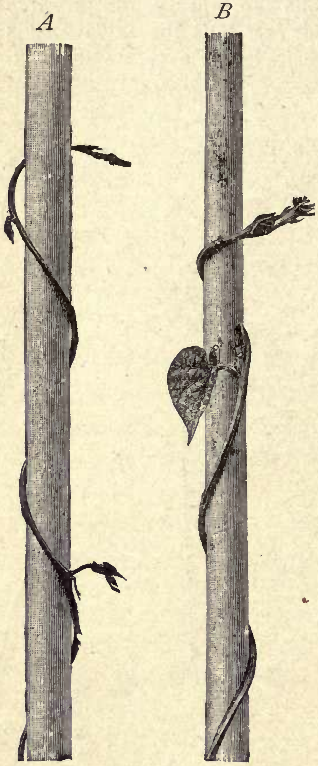


FIG. 135.
Twining stems. *A*, Sinistrorse shoot of *Pharbitis*. *B*, Dextrorse shoot of *Myrsiphyllum*. (After Strasburger.)

But *tendrils* grasp their support as a consequence of contact-stimulus, which reacts by disturbing the growth while young. The tendril is a cylindrical whip-like organ, usually with a hooked tip. Its sensitiveness is sometimes localised along a definite line. During growth it shows movements of circumnutation: if it then comes in contact with a support, inequality of growth causes the tendril to lap round it. (Fig. 136.) Its morphological origin may be various. In the Garden Pea, Vetch, and *Cobaea* it obviously represents the distal region of the leaf, including several pinnae; or it may be the excurrent tip of the lamina, as in *Gloriosa*; or extended parts of the lower region of the leaf may be prehensile, while the lamina or pinnae develop normally after the lower region has grasped the support, as in *Corydalis*, *Clematis*, and *Solanum jasminoides*; or lateral "stipular" structures may be represented by tendrils, as in *Smilax*; or again, the tendril may be referable to a whole shoot, as in the Grape-Vine; and probably a like interpretation may be applied to those of the Passion Flower and the Cucurbits. Thus various parts of the shoot, or the whole of one, may in different cases develop as structures called tendrils, and act as prehensile organs.

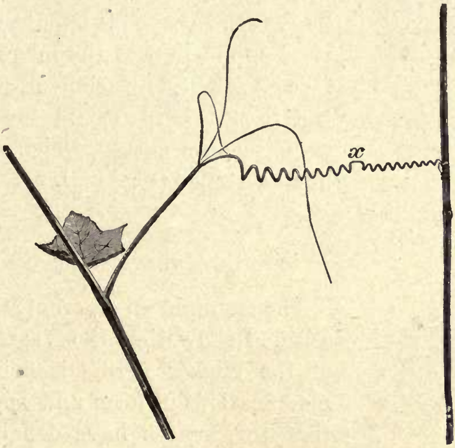


FIG. 136.
Portion of stem of *Sicyos*, a Cucurbit, with tendril attached to support. x = point of reversal of the coiling of the tendril. See Text. (After Strasburger.)

Once they are attached, tendrils strengthen their tissues. As growth ceases, the part between the distal attachment and the base is usually thrown into spiral curves; and as both ends are fixed, these are necessarily equal in number in reverse directions. The elastic tissues of the spirally coiled tendril act like a spring in resisting wind, and recover when the pressure is relieved (Fig. 136).

Adhesive Climbers attach themselves by application of some part of their surface very closely to the surface of the support, following its minute irregularities. The result is that they are affixed so closely that they will often break before quitting hold. *Roots* require little adaptation to this function. The Ivy is a native type of a number of plants of other lands, often large and woody, which attach themselves in this way to tree-trunks, rocks, etc. Such roots of attachment are "adventitious," that is, they are formed not from the root-system, but at points on the shoot, which are usually determined by the external conditions. The roots sometimes lap round the support, with a prehensile action, as in many of the large Aroids.

The familiar case of the Virginia Creeper (*Ampelopsis*) is morphologically identical with its relative the Grape-Vine, but the tendrils are attached by *adhesive discs*. The tips of the branched tendril move away from the light, and this leads to contact with the support: a rock, wall, or tree-trunk. After contact each tip widens into a disc, which at first secretes an adhesive cement. This together with its very close application to the inequalities of surface gives a firm attachment. Subsequently the tissues harden, and the tendril may assume spiral curves, which give a spring-like resistance (Fig. 137).

FIG. 137.
Climbing shoot of *Ampelopsis Veitchii*. The tendrils (*R*) have attached their adhesive discs to the wall-surface behind them. (After Strasburger.)

CORRELATION OF GROWTH.

The examples of external adaptation thus selected show that the Vegetative System of the Higher Plants is liable to various modifications of form and appearance, and that these often have definite relation to the surroundings under which the plant grows. But such modifications are subject to *the limiting principle of Correlation.* Correlation of Growth involves the fact that where one part is developed larger than usual another part is liable to be correspondingly reduced. This applies especially to the shoot, and it may be illustrated by many familiar examples. The succulent stem of a *Cactus* (Fig. 132, p. 176), distended for water storage, bears correlatively small leaves. The same is seen in the swollen tuber of the Potato, with its correlatively reduced scale-leaves (Fig. 138.). An extreme and peculiar case is that of *Welwitschia*, where two enormous plumular leaves increase in size through a long term of years, but the main axis which produced them is atrophied.

Correlation applies not only between leaf and axis, but also between the various parts of the leaf. Thus in the young Broad Bean, and still more clearly in the genus *Bauhinia*, the two basal pinnae develop to a large size, while the distal part of the leaf is represented only by a minute apical spur between them. In *Lathyrus aphaca* it is the

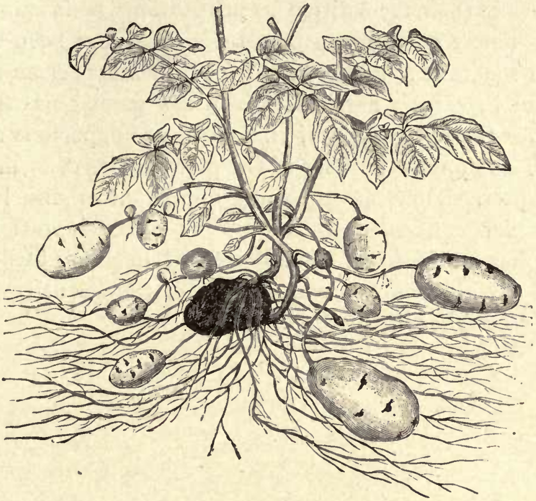


FIG. 138.
Lower parts of a Potato plant, *Solanum tuberosum*. The swollen tuberous stems bear correlatively small scale-leaves. (After Baillon, from Strasburger.)

stipules which become large foliar expansions, while the lamina itself is linear (Fig. 139). In such cases, which might be multiplied indefinitely, *extra development of one part is accompanied by the correlative reduction of another, as compared with normal examples.* But there is no exact numerical *ratio* that can be put upon the proportions. They suggest in general terms, rather than with any exactness, that the excessive expenditure from the total amount of available material on one part leaves a deficiency for others. There is no doubt that this principle of correlation has had very wide application in determining the adult proportions of parts in plants.

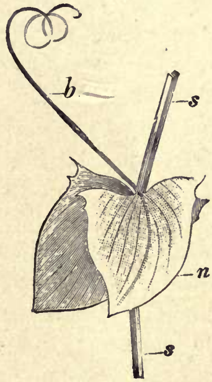


FIG. 139.
Lathyrus aphaca. *s*, stem; *n*, stipules; *b*, leaf-tendril. (½ size.) (After Strasburger.)

Correlation is, however, merely a concomitant of adaptation. It is neither a cause nor an explanation of adaptability, which remains a quite independent problem. It is important to see clearly what is meant when the word "adaptation" is used. It is properly applied to *those special modifications of the plant which arise in relation to the environment.* The advantage which certain features confer upon the plants that show them often appears obvious enough. But it should be realised that their recognition as adaptations is no more than an assumption, unless it is known that their origin has been really connected with the advantage they are seen to confer. Such knowledge is rare, even in cases where the advantage gained seems perfectly clear. Hence the recognition of characters as adaptive is rarely well founded. This applies to many of the peculiarities of form discussed in this chapter. They have been grouped under the heading of adaptations for convenience. The study of "adaptation" is an attractive phase of biology. But it has led to much facile, or even sentimental writing, which has in it little of the scientific spirit, and still less of true scientific method.

CHAPTER XI

IRREGULAR NUTRITION

So far the Plant has been regarded as a self-supporting organism. Starting from the seed with its small supply of food, it has been seen to have the power of acquiring, from the soil and through Photo-Synthesis, the material necessary for its own development. This is the state of regular nutrition shown by most ordinary Plants. Such Plants are called *Autophytes*, and their mode of life *Autotrophic*. Some Families are composed entirely of these, for instance the Grasses and Crucifers. There is little doubt that complete *self-nutrition* was a characteristic of the most primitive vegetation.

But there are many plants which are *Heterotrophic*, that is, they show some *irregular or accessory method of nutrition*. They are able to derive organic nourishment from some source outside their own body. Some such plants are only partially dependent upon irregular nutrition, others are wholly dependent upon it; while the method of supply is also subject to considerable variety in different cases. For instance, the food supply is sometimes taken from some other *living organism*. This may be either a Plant or an Animal, and it is called the *Host*, while the dependent organism is called a *Parasite* upon it. But sometimes the dependent organism feeds not upon the living host, but upon the *dead body, or upon the products of its decay*. Such a dependent is called a *Saprophyte*. There is no sharp line that can be drawn between these two conditions, for sometimes the parasite causes death, but continues to feed upon the corpse. Thus it would be first a parasite, and afterwards a saprophyte. The converse may also happen. A peculiar place in this respect is taken by those *Carnivorous* plants which digest small animals. They capture the living animal, but feed upon its dead body. Other cases exist where two organisms may live together with mutual tolerance, or advantage, as in the Lichens. This has been described as *Symbiosis*, or *Mutualism*. There being thus a wide range of variety in these states of dependence, the subject will be best approached through the description of actual examples rather than by general statements.

There is, however, one fact which is common to them all. *Contact with the source of supply* is necessary for the establishment of any of these conditions. A crowded vegetation naturally favours this. The matted roots of any sod give the opportunity for *root-parasitism*, such as is seen in the Yellow Rattle; the close contact of climbing plants with their support offers facilities for *stem-parasitism*, as in the Dodder. The growth of various Algae attached to the submerged surfaces of water-plants, or it may be actually in the intercellular spaces of aerial parts, are common examples of close contact. This state has probably led on from mere association to that physiological dependence which is seen in certain Fungi. The decaying remains of a crowded vegetation persist for a long time as *humus* or *leaf-mould*, which itself supplies the most common source for saprophytic nourishment. The advantage which the dependent organism gains, by getting nourishment without needing to manufacture it for itself, offers a ready explanation of the frequency of these phenomena.

Irregular nutrition is not restricted to any one Family or Group of Plants, but it has become the leading character of some of them. The *Fungi* are the chief examples of it. But as they are very highly specialised in this relation, while the fossil history shows that irregular nutrition was established very early in them, they will be held over for special study in later chapters (XXVI.-XXIX.). For the present the illustrations will be taken from the Flowering Plants. Some families of them appear to be specially prone to physiological dependence. For instance, the Loranthaceae, and Orobancheae. In other cases isolated genera have adopted the habit; for instance, the Dodder among the Convolvulaceae, or *Cassytha* among the Laurels. Such facts lead to the conclusion that *irregular nutrition among Flowering Plants is a relatively late and sporadic advance upon the primitive state of nutrition characteristic of the Green Plant.*

Partial Parasites.

Certain plants which have adopted a parasitic habit still retain their chlorophyll, though their colour is apt to be yellowish rather than the full green. They are thus able to carry on Photo-Synthesis, and to produce at least part of their own nourishment. They are only partial parasites. This state is seen in the Loranthaceae, with the familiar example of the Mistletoe (*Viscum*), a plant which grows fixed on the branches of various trees. It occurs occasionally on the Oak, on which it was in early days recognised as the mysterious "Golden Bough." Other native green parasites are the Eyebright (*Euphrasia officinalis*), and the Yellow Rattle (*Rhinanthus crista-galli*), while *Cassytha*, a very omnivorous parasite of the tropics, has also a green colour.

These plants are all fixed by means of *haustoria* or *suckers* upon the host-plant in such a way that the tissues of the one come into close relation with the tissues of the other. In the case of Eyebright and

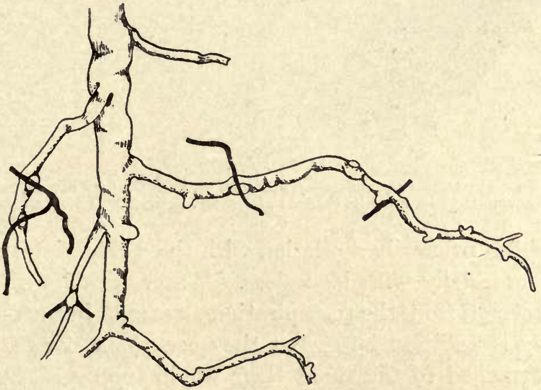


FIG. 140.
Root of Louse-wort (*Pedicularis*), which like Eyebright and Yellow-Rattle, is fixed by suckers upon the roots of the host, here represented black. (After Maybrook.)

Yellow Rattle there are suckers upon the roots, and they penetrate the roots of the grasses with which the plant grows. The close juxtaposition of the roots in the sod offers a ready opportunity for the parasite (Fig. 140). The effect of the parasitism upon the Grasses in a meadow is such that patches infested by Yellow Rattle can often be recognised from a distance by the poverty of their growth. In *Cassytha* the suckers arise from the shoot, and the close vegetation of the tropical undergrowth gives the necessary contact at many points. In the case of Mistletoe, and of its near relative *Loranthus*, the opportunity for parasitic attachment arises from the fact that their fruits are viscid; in fact Bird-Lime is derived from them. The berries are eaten by birds which reject the sticky seeds, leaving them attached to the twigs on which they perched. Here the seeds germinate, and their roots penetrate the living tissues of the host. In *Viscum* a suctorial system spreads from the original centre, within the tissues of the host, penetrating along the region of the cambium. But in *Loranthus* the shoot of the parasite creeps along the outside of the host, and puts in suckers at intervals (Fig. 141).

There may thus be differences in the method of the attack; but in all of these green parasites the physiological position is the same.

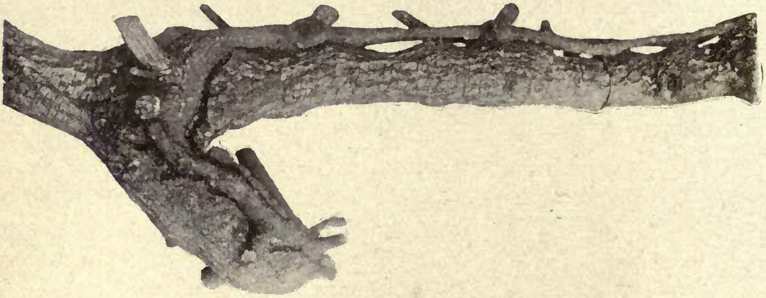


FIG. 141.
Loranthus parasitic externally upon a branch of the Alligator Pear, by means of haustoria penetrating its tissues at intervals. Ceylon. (½ Natural size.)

They establish primarily a relation with the conducting system of the host, and especially with its xylem. Water with its dissolved salts is then drawn off from the transpiration-stream. In the root-parasites this supply is additional to what they can themselves absorb. But in those attached to the shoot their whole supply is thus obtained. It is uncertain whether or in what degree organic supplies may also be abstracted. In any case the presence of chlorophyll shows that these green parasites are not wholly dependent upon their host, but can themselves carry on Photo-Synthesis.

COMPLETE PARASITES.

In these, though the plant may show various colours, the green of chlorophyll is absent, and they are entirely dependent upon the host for the supply of organic as well as inorganic food. A familiar example is the Dodder (*Cuscuta*), a genus represented in the British Flora by three species. It belongs to the Convolvulaceae, and shares with *Convolvulus* the twining habit (Fig. 142). Clover fields are sometimes attacked by one of these Dodders (*Cuscuta trifolii*), and the infected patches can be seen from a distance by the reddish colour of the parasite, and the stunted growth of the clover upon which it preys. Examination shows the Dodder to have cylindrical stems, which twine closely round the host plant, and are attached by numerous suckers along the surface of contact. Though the seedling germinates in the soil, the parasite after making its attachment to the host, loses its hold on the soil. It thus becomes entirely dependent on the host for its

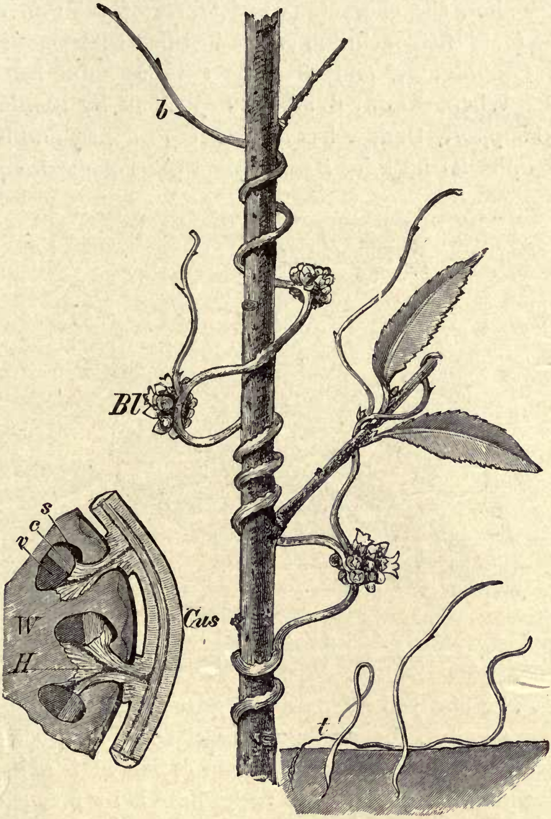


FIG. 142.

Cuscuta europaea, on the right germinating seedlings. In the middle a plant of *Cuscuta* parasitic on Willow: *b*, reduced leaves of the floral region; *Bl*, flowers. On the left cross-section of the host, showing haustoria, *H*, in intimate contact with the vascular strands. (After Strasburger.)

supply of water and soluble salts. Since it has no chlorophyll, it is also dependent on the host for its organic supply. It is in fact a complete parasite.

A marked feature is the absence of foliage leaves in the vegetative region of the Dodder. There are not even any cotyledons on the embryo. This is to be connected with the parasitic nutrition; there is no self-nutritive function necessary in the parasite, and the leaves which normally carry it on are not required. *Such reduction of the vegetative system is usual in complete parasites.* But this reduction does not apply to the floral region. The flowers of the Dodder, which are produced in dense heads, arise each in the axil of a bract, and structurally they show the characteristic features of the Convolvulaceae. From these facts the conclusion seems justified that Dodder is a type related to Convolvulus, and that the twining habit has led to its parasitism. Whereas Convolvulus is dependent by twining only for mechanical support, Dodder has gone a step further, and has become dependent upon its host for its complete physiological support also.

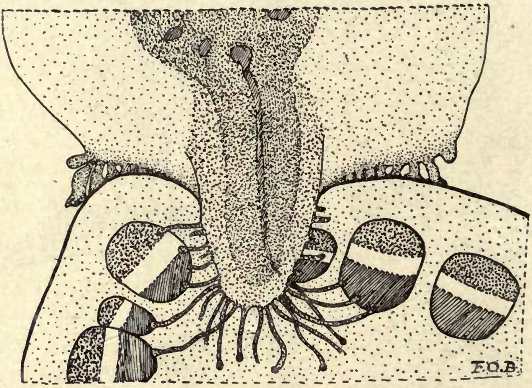


FIG. 143.
Cuscuta europaea. Section vertically through a sucker, which projects from the stem of the Dodder, shown above in the drawing, into the stem of the host. See Text. (× 35.)

Further, as it is an isolated parasitic genus, and its flowers are like those of Convolvulus, though on a smaller scale, it appears probable that its parasitic habit has been acquired relatively late in its evolution.

The attachment of the Dodder to its host is by means of suckers, which probably represent highly modified roots. The details of the connection appear to be variable in different species, and perhaps on different hosts. In specimens of *Cuscuta europaea* the facts appear strongly to support their root-character (Fig. 143). First an adhesive disc projects from the stem of the parasite, and becomes closely appressed to the surface of the host, attaching itself by rhizoid-like hairs. Endogenous tissues then burst through like a root, and penetrate the tissues of the host. The superficial cells of the penetrating sucker then grow out into tubes of varying length. Some of these apply themselves to the wood, others to the bast, others to the pith and cortex, thus tapping both storage and conducting tissues. Where the sucker impinges upon a vascular strand a continuous xylem-connection may be established; in the phloem also a close relation of the sieve-tubes of the parasite with those of the host has been shown.

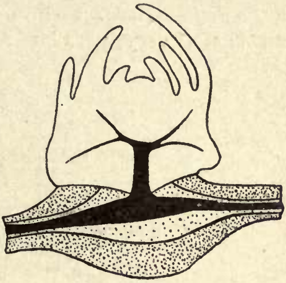


FIG. 144.
Median section of a young plant of *Orobanche* seated upon the root of its host. (After Hovelacque.) (× 20.)

The Broomrape (*Orobanche*), and the Toothwort (*Lathraea*) are further examples of parasites with complete physiological dependence. Both of these are root-parasites, with attachment to the host by haustoria, which penetrate the tissues. The Toothwort which infests the roots of Hazel is classified in the Scrophulariaceae, close to the Eyebright and Yellow Rattle, which are themselves partial root-parasites. But it differs from them in having become entirely dependent physiologically upon its host. The leaves are still represented on the underground shoot, and their curiously reduced and altered form gives rise to the name of Tooth-Wort. But the flowering shoot rises above ground, displaying flowers with structure characteristic of the Family.

FIG. 145.
Flower-buds of *Rafflesia* bursting their way out from the root of *Cissus*. (After Robert Brown.) Much reduced.

The Broom-rapes (*Orobanche*), which attack various plants, woody or herbaceous, are closely related to *Lathraea*. They show a greater modification of the shoot, which attaches itself on germination to the root of the host, developing a brown tuberous body, without leaves, and shut off from the light. By means of a sucker it burrows with a broad surface into the root of the host plant, and establishes a close relation with its conducting tissues (Fig. 144). The flowering shoot with its brownish leaves rises above ground, bearing numerous flowers. Their structure shows that it is a form related to the Toothwort, but its vegetative system is still more reduced, leaves being absent from the base of the tuber. This reduction runs parallel to but distinct from that seen in Convolvulus and Dodder. The two sequences provide a good example of *homoplasy*, or parallel development, and show that parasitism may originate separately in distinct families, though the steps of the consequent modification may be alike.

An example of a still further reduction of the vegetative system of a complete parasite is seen in *Rafflesia*, which grows enclosed within the tissues of its host. It infests the stems and roots of *Cissus*, traversing the tissues with branched filaments of cells. At first there is nothing that can be recognised as stem, leaf, or root. The vegetative system is reduced to the level seen in parasitic Fungi. But when flowering follows, large buds are formed deep down in the tissue of the host. These burst through, and develop as flowers (Fig. 145). In *Rafflesia Arnoldi* each flower is thirty inches across when full blown, and has a very peculiar and complex structure (Fig. 146). It thus

FIG. 146.
Flower of *Rafflesia Arnoldi*. Much reduced. (After Robert Brown.)

appears that while in parasites the vegetative system shows reduction, which may at times reach an extreme, as in *Rafflesia*, the flower may nevertheless be disproportionately large and elaborate, and produce very numerous seeds. Biologically their number may be held as an offset to the risk of not finding the proper host on germination.

MYCORHIZA.

Many Plants which look like normal autophytes prove on examination to have irregular nutrition, following on a state which is called *mycorhiza*. But this, as it more particularly affects the roots, may not be visible above ground. Trees such as the Beech, Hornbeam, Oak, and Scots Pine are examples. In certain families it is prevalent, as in the Heaths and Orchids. A similar mode of nutrition is often present in the Club-Mosses and the Adder's-tongue Ferns, and it occurs also in some Liverworts. Thus it is not restricted to any single family, or even group of Plants.

It consists in *a coalition between fungal filaments and the living tissues of another plant*. Fungi have special powers of absorption of certain substances from the medium in which they grow. They extract soluble salts readily from the soil. They are also able, in accordance with their usually saprophytic life, to acquire organic material in the combined form from a substratum which contains it.

In these respects Fungi are better equipped than ordinary green Plants, and it is this which makes a coalition with them a physiological advantage. Mycorhiza may even lead indirectly to a state of saprophytic nutrition.

Two different types of this coalition are recognised. In the first the fungus lives outside the tissues of the plant with which it is related; this is described as *ectotrophic*, and it occurs in the Beech, Hornbeam, Oak, and Scots Pine; also in *Monotropa*, and *Sarcodes* (Fig. 147). In the second the fungus penetrates the tissues, and it is accordingly styled *endotrophic*; it occurs in the Heaths and Orchids, and in the Club-Mosses and Adder's-tongues.

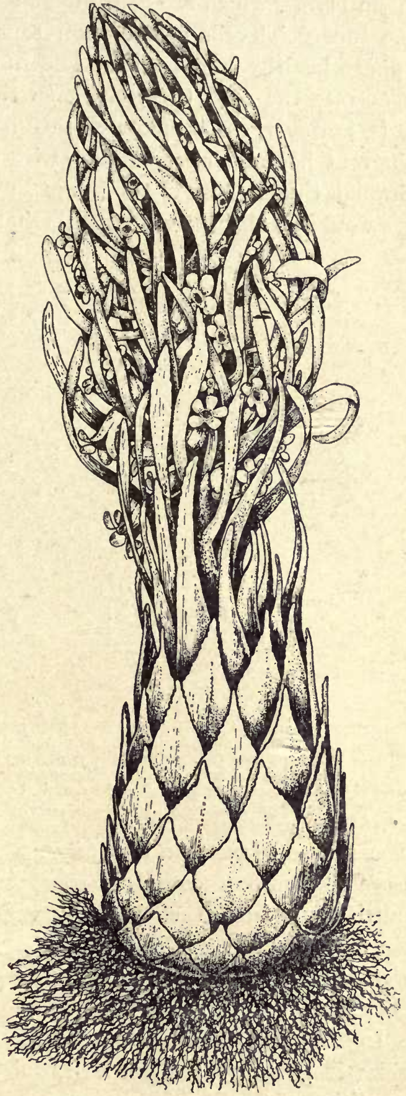


FIG. 147.
Whole plant of *Sarcodes*, showing the mycorhizic root-system, from which arises a bulky flesh-coloured shoot, with broad sheathing scales below, and a terminal inflorescence with prominent bracts. Reduced. (After Oliver.)

(*a*) ECTOTROPHIC MYCORHIZA.

Externally roots showing *ectotrophic mycorhiza* appear wrapped round by a covering of fungal origin, and are short and thick, and repeatedly branched. The branching is sometimes endogenous as in ordinary roots; but in other cases it is of external origin, with transition to forking in the Scots Pine. Sections show that the roots are covered by a thick felt of matted fungal threads, which sometimes stop short of the tip (*Monotropa*), but usually cover it completely (*Pinus*, *Fagus*, *Carpinus*, *Sarcodes*) (Fig. 148). In the last-named, which is a complete saprophyte native of the Western States of America, the root-cap is shed off in layers, which are held in the fungal weft. This closely invests the superficial cells of the root, forcing them apart; but still they appear healthy and active. The fungal filaments do not as a rule penetrate the cells themselves, so that the investment is external. It is, however, so complete when fully developed that the surface of the root has no direct contact with the soil, and takes its supplies through the medium of the fungus. The hyphae at the outer surface grow out into absorptive filaments that take the place of the root-hairs.

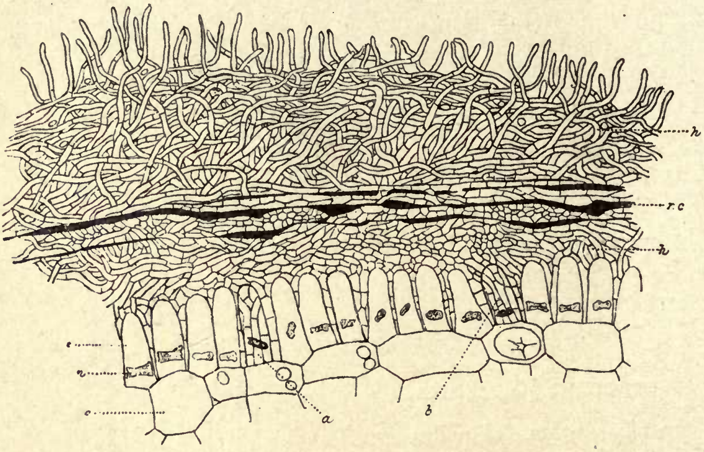


FIG. 148.

Part of the superficial tissue of a root of *Sarcodes*, covered by a dense felt of fungal hyphae (*h*), in which the dark lines (*r*, *c*) are the layers of the root-cap. The outermost layer of cells of the cortex (*c*) is covered by a piliferous layer (*e*), but the root-hairs are replaced by conical cells between which the fungal hyphae have forced their way. (After Oliver.)

The native *Monotropa hypopitys*, which grows in woods of Fir and Beech, is also a complete saprophyte. Its only visible means of nutrition is from the decaying vegetable matter in which it lives, through the intermediary of the symbiotic fungus. This is found closely investing the surface of its roots, and occasionally penetrating the cells.

In estimating the relations of the two parties to ectotrophic mycorhiza in green plants, one essential fact is that it is not a necessary condition of the life of the tree, nor does the fungal investment necessarily cover the whole root-system. Experimental cultures have given contradictory results as to the benefit derived by the higher Plant. But certain general considerations seem clear. On the side of the fungus, which is already leading a saprophytic existence in the soil, a direct supply of carbohydrate will be obtained by contact with the root. The initial advantage from the coalition would then lie with the fungus. The advantage which the trees derive is in the first place the more ready supply of salts, and of combined nitrogen extracted by the fungus from the soil. The hyphae establish a more intimate relation with the soil than ordinary root-hairs, and there is abundant evidence of their special aptitude for absorption not only of such salts, but also of organic materials. These also they may hand on to the root. That the relation is mutually satisfactory is shown to be probable by its prevalence, and by the vitality which both the parties show.

But the importance of this form of irregular nutrition varies greatly for different plants. It culminates in those cases, such as *Monotropa* and *Sarcodes*, in which the plant is almost, or entirely without chlorophyll of its own. Clearly the supply of all organic material, as well as of water and necessary salts, is here obtained through the fungus from the humus substratum. It may not perhaps be strictly true to call these plants themselves saprophytes; but the legal maxim runs, "*qui facit per alium facit per se.*" *They are physiological* "*resetters*"; that is, saprophytes at second-hand, *being actually parasitic on a saprophytic fungus.* It is quite possible that in less degree the same may be the case even for the Beech, Oak, and Scots Pine.

Endotrophic Mycorhiza.

The essential feature of *endotrophic mycorhiza* is that *fungal filaments occupy the living cells of the host, coming into intimate relation with their protoplasts.* It is stated that occasionally the ectotrophic fungus of *Monotropa* or *Sarcodes* may penetrate the superficial cells, a fact which suggests how the more prevalent endotrophic type may have arisen. It is characteristic of Orchids, and Heaths, and is found in many isolated genera, such as *Paris*, *Anemone*, and *Allium*, and among such lower plants as *Psilotum*, *Lycopodium*, and the Ophioglossaceae. A similar condition is also seen in some Bryophytes. There is great variety in the colouring of these plants. Most of them show a full green, and would pass perfectly as autophytes; as for instance *Rhododendron*, the Heaths, or *Paris*. Some are more or less pale in colour, as in such Orchids as *Goodyera*, or *Listera cordata.* Others may be without chlorophyll, showing a brownish tinge, as in the Bird's Nest Orchis (*Neottia*), or the Coral-Root (*Corallorhiza*). These differences suggest different degrees of dependence for organic supply upon some other source than Photo-Synthesis. That source is some fungus which lives within the plant. The fungal filaments are able to penetrate the cell-walls, and pass readily from cell to cell. Usually they are massed in certain zones, especially in the cortex, and are coiled within each cell, the protoplast and nucleus of which still retain their vitality. This indicates that a *mutual life* is maintained—a condition of *symbiosis*.

The Heath Family shows generally a mycorhizic condition. The hyphae are present not only in the root of the Common Heather, but also in the stem and leaves, and extend even to the ovary, where they may be traced as infecting the seed-coat. The germ is free from them in the seed, but infection takes place shortly after germination.

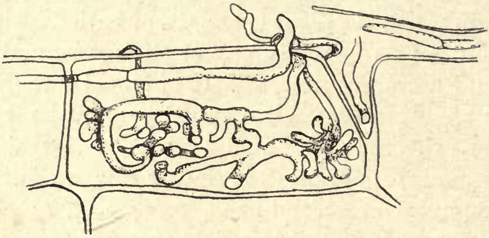


FIG. 149.
A single superficial cell of the young root of Common Heather (*Calluna vulgaris*) showing the endotrophic fungus, and its penetration of the cell-walls. (After Rayner.) (× 1500.)

Without the fungus, as shown by pure sterile cultures, the seedlings do not develop roots, and though they remain alive for months their growth is stopped. On infection with the right fungus they develop normally. Thus the synthesis of fungus and plant has been experimentally accomplished. The conclusion is that *the Symbiosis is a necessary condition of normal life in the Common Heather.* Similar fungal infection of the seeds in the ovary is the rule in other Ericaceae examined.

The outside of the young root of Heather consists of a single layer of large cells, with reduced cortex and a slender vascular strand within. Root-hairs are absent. The outer surface is covered by septate and branched hyphae, which often grow between the cells, while some penetrate the walls. Within the cells they develop several stout coils, with here and there short thick branchlets, completely filling the cell (Fig. 149). In stem and leaf the fungus is found among the superficial hairs, while hyphae penetrate even the cuticularised walls. They enter the epidermis, mesophyll, and cortex, and accompany the vascular strands. The mechanism at least is here present for the fungus to act as a physiological intermediary between the Heather and its surroundings. Possibly the fungus is able to fix atmospheric nitrogen in some degree. In the root it is also in connection with the soil, which is as a rule heavily organic where the Heather grows. It would thus be in a position to supply organic material and combined nitrogen. The entry of the fungus

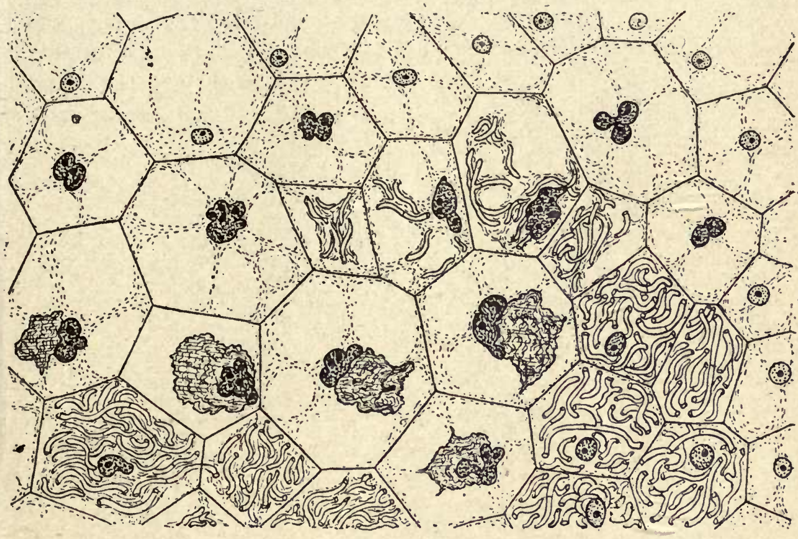


FIG. 150.
Section through the mycorhizic region of the tuber of *Phalaenopsis*. At the top of the figure are normal cells of the host: at its lower limit are cells crowded with fungal filaments, but still retaining their nuclei. Between these zones is the digestive tract, consisting of cells with lobed nuclei. Various stages of digestion of the fungal filaments are seen in these cells. (After Bernard.) (× 98.)

into the host may originally have been parasitic, but it is tolerated. In the Heather it has even become indispensable. *By means of the symbiosis many Ericaceae " have solved the problem of growth on poor and unpromising soils, but have solved it at the price of their independence "* (*Rayner*).

A similar relation has also been demonstrated in a number of Orchids, and it may be held as a general feature of that family. The fungus in question is filamentous, and septate, and lives symbiotically in the cells of the host. It is referred to the genus *Rhizoctonia*, and three species have been recognised. In certain cells the fungus remains permanently active. *But other cells of the host, which may accordingly* *be called "phagocytes," are able to digest the fungus.* They may be recognised by having lobed nuclei, as seen in Fig. 150. On the one side of the digestive tract are normal cells of the host; on the other there are cells of the infected region which continue to act symbiotically. They retain the simple nucleus, and do not attack the fungal

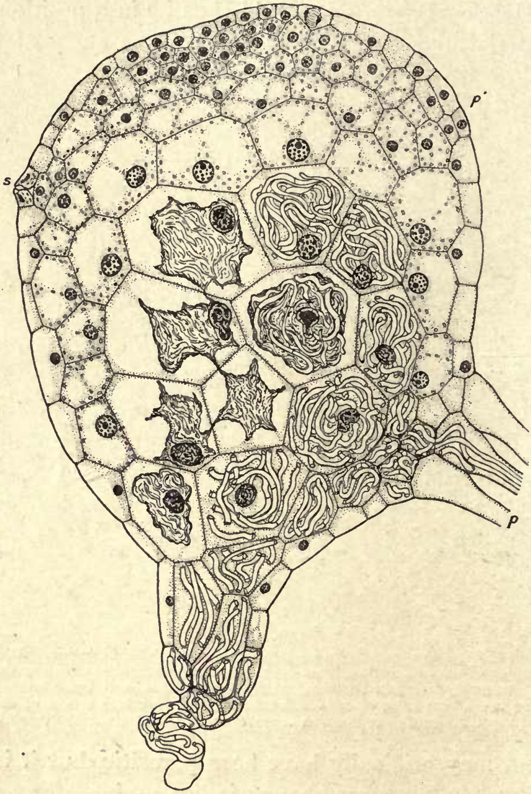


FIG. 151.

Median longitudinal section of a young plant of *Odontoglossum*, one month after infection by *Rhizoctonia*. s = stoma; p = group of absorbing hairs; p' = cells divided tangentially, of which the outer will form hairs. Digestion as in Fig. 150; the apex is not infected. (After Bernard.) (× 120.)

filaments. The phagocytes thus serve as a barrier, limiting the infected area, and checking the spread of the fungus into undesirable parts, such as the conducting tracts, or the apical points. At the same time *the organic materials of the digested fungus are absorbed into the host plant.* Connection between the undigested filaments within and the soil without is meanwhile maintained by tufts of superficial hairs arising from either stem or root. Through these the hyphal filaments pass, either outwards to establish connection with the humous soil, or inwards to cause new infections. (Fig. 151, *p.*)

Within the Orchid family there is some variety in the application of this indirect nutrition. In some cases (*Bletiella*), germination is independent of the infection of the seedling, which need not occur till several leaves have been formed. In the Ophrydeae, which include most of the native ground Orchids with tuberous stocks, the infection is very early. It causes that tuberous swelling of the sympodial stock and roots, which is repeated in each annual growth of these plants (Fig. 152). Most of the Orchids that are thus mycorhizic possess chlorophyll, giving them a more or less full green colour. They are thus only partially dependent upon the symbiosis.

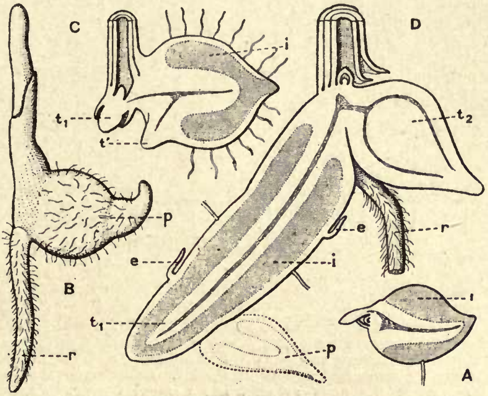


FIG. 152.

Germination of the Ophrydeae. *A* = young tuber of *Orchis* in section. *B* = young plant. *C* = young plant of *Ophrys* in section. *D* = diagram of young plant of *Platanthera*, second year; *p* = tuber of first year; *t, t* = succeeding tubers; *e* = scales; *i* = infected region; *r* = root. (After Bernard.)

But others are wholly dependent, growing as complete saprophytes. The most important native examples are *Corallorhiza* and *Neottia.* The former grows in Pine woods with its rhizome embedded in rich humous soil. It consists of freely branched underground shoots, bearing scale-leaves, but no roots. The aerial part of the plant is a simple scape, bearing only colourless scales, and at the top a raceme of small pale flowers. The fungus gains access to the tissues through the numerous tufts of hairs scattered over the surface of the shoot. Digestion of the hyphae has been observed, and as they disappear starch-grains are formed in the inner tissues.

The relation of host and fungus has been worked out very fully in the *Bird's Nest Orchis* (*Neottia*), which grows commonly in woods, putting up its brown flowering scape in early summer. If it be dug up, the brown "bird's nest" is found to consist of thick fleshy roots crowded upon a short central axis which bears scale leaves, with lateral buds in their axils. It is, in fact, a rhizome, as in *Corallorhiza*; but whereas roots are absent here, in *Neottia* they form the most prominent feature (Fig. 153 *C, D*).

Externally no fungus is obvious, but if sections of the root be cut the third to the fifth layers of the cortex have their cells crowded by coiled fungal hyphae, which are enclosed in the still living nucleated protoplast. The infec-

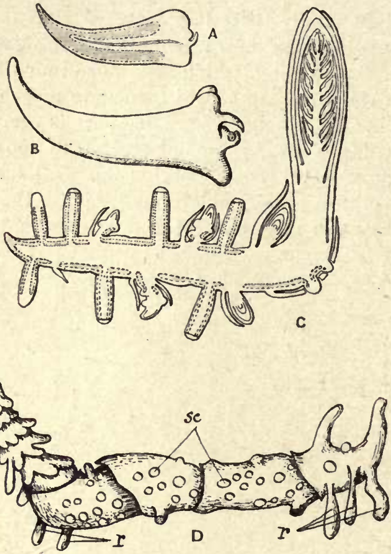


FIG. 153.

Neottia nidus-avis. *A* = young tuber in section showing infected region shaded. *B* = rather older plant seen from outside. *C* = diagrammatic section of plant at period of flowering, showing scale-leaves, axillary buds, and the insertion of the prominent roots. The infected regions are shaded. *D* = rhizome seen from outside, with roots removed: the scars (*cs*) show how numerous the roots are. (*A*, *B*, *C* after Bernard; *D* after Irmisch.)

tion has been found to start with the germination of the seed, and is probably not repeated (Fig. 154). Tufts of hairs, such as are present in *Corallorhiza* and many other Orchids, are absent: but communication is kept up with the soil by occasional hyphae which traverse the superficial cells. According to

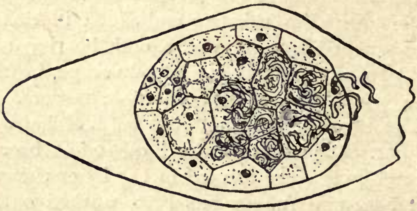


FIG. 154.

Seed of *Neottia* infected by fungus, and showing the first stages of germination. (After Bernard.) (× 100.)

age and position the fungal filaments show various stages of disorganisation. In some cells only the indigestible remnants of the hyphae remain. The nuclei of the digesting cells meanwhile increase in size, and starch appears in quantity in the cortex. All these indications show that *the materials of the digested fungus have been absorbed into the host-plant.*

The saprophytic Orchid *Gastrodia*, which grows in Oak woods in Japan, provides another example. The plant consists of colourless and rootless tubers, which may bear small daughter tubers as offsets. The inflorescences are borne only by tubers of large size, and they are found to be invariably infected by rhizomorphs of *Armillaria mellea*, which preys on the roots of the Oak trees. The Rhizomorphs ramify on the surface of the infected tuber, and penetrate through its corky coating by haustoria curiously similar to those of *Cuscuta*. The infection spreads laterally in the cortex, but does not penetrate deeply, being checked by the active resistance of the inner layers, which not only control, but also digest and absorb the substance of its hyphae. It thus appears that while the Rhizomorph is dependent upon the Oak, the *Gastrodia* is parasitic on the fungus, and depends upon that parasitism for its successful flowering. It is a case of parasitism at second hand. The attack of the Rhizomorph is tolerated, and kept under control by the resistant powers of the *Gastrodia*, so that the would-be assailant, itself a parasite, is compelled to disgorge. The success of the whole arrangement depends upon the resistant powers of *Gastrodia* being greater than those of the Oak.

It seems probable that in the coalition called endotrophic mycorhiza the initiative came from the fungus, by penetration from the soil into the tissues of the host-plant. The plant at first defended itself by the digestive process, by which the intrusive fungus was kept within bounds, and headed off from tissues of vital importance. Incidentally, however, the plant gains materials by the digestion which are of value for its own nutrition. The nourishment acquired by the fungus is first worked up into the substance of its own well nourished hyphae. These are then digested by the higher plant into which it has penetrated, and converted to the uses of the host. Such host plants may be styled "*fungivorous*," in a sense parallel to those plants which have adopted a *carnivorous* habit. *But a nearer parallel is probably to be found in that intra-cellular digestion, seen in the* AMOEBA: *or in the behaviour of the* LEUKOCYTES *of the animal body, which is a leading feature in* "PHAGOCYTOSIS."

An association such as that of *Neottia* with the fungus *Rhizoctonia*, or of *Calluna* with its *fungus*, should not be regarded as an individual. It is rather to be compared with a Lichen, being like it an obligatory product of two distinct organisms. Such *symbiotic conditions* as these occupy a middle position between two extremes. The one is that of *mortal disease*, where one organism of an association causes the ultimate death of the other. The other extreme is that of *immunity*, where though two organisms may be in relation, the one has no power against the other. An intermediate state between these extremes is realised in nature when two antagonistic organisms, by balancing their powers, attain to *a life of mutual toleration* lasting for a prolonged period, as in Lichens, or mycorhizic Flowering Plants. The number of such associations now recorded has rapidly increased in late years, while varying degrees of dependence, and of toleration or obligation have been detected.

It appears further that there may be variation from time to time in the aptitude of the attacking organism for living with its host. In the case of *Rhizoctonia* it has been shown that by an autonomous life it gradually loses its power, or even becomes incapable of causing the seeds of the Orchid to germinate. On the other hand, it increases that power by living with its host. This varying aptitude for symbiosis seems in every way comparable to the *varying virulence of pathogenic organisms.* Similar variations in the power of attack were demonstrated long ago by de Bary in the case of *Sclerotinia*, and other cases are known among pathogenic Fungi.

Both in ectotrophic and in endotrophic mycorhiza various steps are illustrated between partial and complete physiological dependence. Where the dependence is partial there is little or nothing in the appearance of the plants above ground to suggest irregular nutrition; excepting in some cases paleness of colour, which indicates imperfect development of chlorophyll. The complete result is shown on the one hand by *Monotropa* or *Sarcodes*, on the other by *Corallorhiza* or *Neottia.* In both cases chlorophyll is absent. There must then have been an indirect supply of organic material from the humus outside. The fungus supplies the intermediate step. It thus appears that *both types of mycorhiza culminate in complete Saprophytism at second hand.*

Root-Tubercles.

The formation of tubercles upon roots, and their importance in the fixation of Nitrogen has already been mentioned in Chapter VII. p. 106. Such tubercles are found almost universally in the Leguminosae, and similar growths are also known in the roots of other plants, such as the Alder Tree. It will be seen that these tubercles have much the same physiological significance as mycorhiza, and like it involve digestion of the intrusive organism.

In any ordinary crop of Beans the roots are found to bear numerous tubercular swellings, often of large size and irregular outline (Fig. 155). Dissection shows that they are seated just outside the stele, and may when young be mistaken for lateral roots, since they arise from the same spots as roots, and vascular tissue extends from the stele into them as they mature. But their structure is different from that of roots (Fig. 156). They consist chiefly of parenchyma, which when young is found to be traversed by thread-like bacterial masses, extending from cell to cell. From these masses numerous minute bodies are derived, which crowd the cells of the tubercle, but do not destroy the protoplasts, while the nuclei of the cells remain well nourished and of large size (Fig. 156, 2). In annual Leguminosae the greatest development of these bodies in the cells is reached about the time of flowering. But from this time onwards their numbers diminish. Most of them become dissolved, and the evidence indicates that their organic materials are drafted off into the conducting system of the host. When the seeds of the Leguminous plant are ripe the nodules have shrivelled, and relatively few of the small bodies remain. These are set free into the soil as the nodules rot. The bodies thus set free are rod-like and motile, and are called *Bacterium radicicola*. These *Bacteria* have been cultivated apart from the plant, and it appears that in presence of proteid and sugar they are able to bring the free nitrogen of the air into combination.

FIG. 155.
Root of *Vicia Faba*, with numerous root-tubercles. Reduced. (After Strasburger.)

The infection of the roots has been traced to the root-hairs, and doubtless the infective germs are derived from the former tubercles rotted in the soil. A bright spot appears close to the tip of the root-hair. This is a small mass of that gelatinous state of Bacteria known as the zooglaea stage. It works its way through the cell-wall into the cell, and extends downwards as the thread-like body already noted (Fig. 156, 3). It traverses the cells of the cortex to the point outside the stele, where the tubercle arises. Cell-division is stimulated, and the zooglaea disintegrates, while the Bacteria multiply greatly, filling the cells. Most of them assume a branched and turgid form, and are distinguished as "*Bacterioids*." These are digested by the cells in which they developed, and their materials are used by the host-plant.

Experiments have shown that Leguminous seedlings grown in sterilised sand, to which a full food-supply exclusive of combined nitrogen has been added, fail from want of nitrogen. Like any other green plants they are unable to use the free nitrogen of the air. But

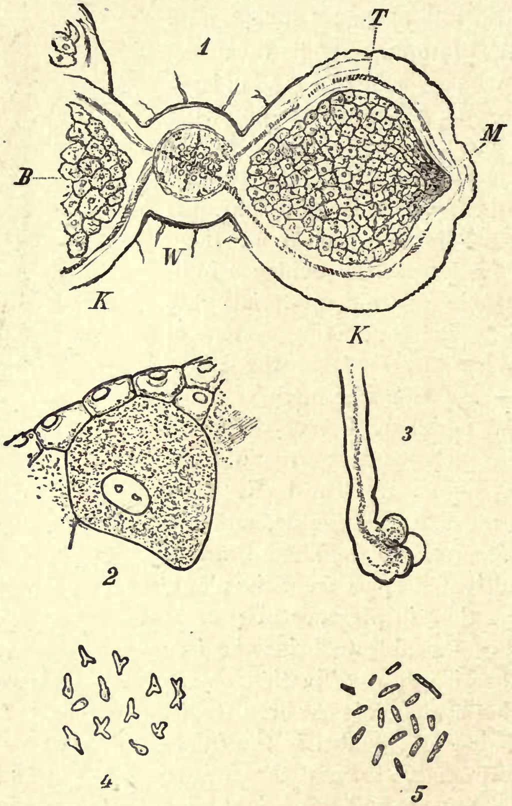


FIG. 156.
Young tubercles (*K*) on a root (*W*) of *Vicia Faba*. *B*=large-celled tissue filled with masses of Bacteria. *M*=meristem. *T*=tracheides. (× 60.) 2, a cell infected with bacteria, and smaller non-infected cells. (× 320.) 3, an infected root-hair. (× 320.) 4, Bacterioids. 5, unaltered Bacilli. (× 1200.) (After Strasburger.)

if a water-extract of ordinary soil be made,—especially if the soil has lately grown similar Leguminous plants,—and if it be added to the culture, the plants will thrive with all the evidences of a sufficient nitrogenous supply, while a free development of tubercles takes place upon the roots. Moreover, analysis shows that the nitrogenous content of the tuberculous plants is increased by the co-operation of the two organisms. But it is still uncertain how this is done. It has been seen that in pure culture the Bacterium can in some degree fix free nitrogen from the air. The roots would supply the sugar and proteids necessary for the process. Possibly the coalition of the two living organisms in some way encourages it. Finally the digestion of most of the "Bacterioids" by the living cell in which they had developed, secures the transfer of the nitrogenous compounds acquired to the higher plant. *This is again a case of "Phagocytosis," but here it follows on active fixation of nitrogen from the atmosphere.* The importance of this in Agriculture is obviously very great, for the supply of combined nitrogen is the most difficult problem of the farmer.

Carnivorous Plants.

The predatory methods of Carnivorous Plants have been considered from the point of view of the reception of stimulus, and the consequent movements, in Chapter VIII. Another aspect of them is in respect of nutrition. The plants which show this peculiar habit grow under conditions where the supply of combined nitrogen is difficult, such as in peaty or humus soil, where the native *Pinguicula* and *Drosera* are habitually found. Venus' Fly Trap and *Sarracenia* grow on boggy moors in America, while *Nepenthes* is an epiphyte. In such positions nitrates and other salts would naturally be deficient. On the other hand, all of these plants contain chlorophyll, and can thus construct carbohydrate for themselves. In point of fact the carnivorous habit is not essential to their existence, though experimentally it is found that a moderate supply of animal food is beneficial.

Apart from the mere mechanism of capture, which is very various, the physiological treatment of the prize is fairly uniform. Its success depends upon secretion of digestive juices from certain localised, glandular cells. This has been studied very thoroughly in the Sundew (*Drosera*), in which the mechanism of capture has already been described (p. 131). The secretion which plays so important a part is produced by the glandular head of the tentacle, which receives its vascular supply through a strand traversing its stalk. (Fig. 157.) The viscid secretion is exuded by the epithelium that covers the surface of the gland. On contact with an insect, or with a small piece of nitrogenous matter, such as a cube of white-of-egg, the gland is stimulated to greater secretion. A proteolytic ferment, which breaks down the complex proteid to simpler soluble substances, is given out, and the secretion takes an acid reaction. The emission of the ferment and of the acid is, as in the gastric secretion of the animal stomach, dependent upon the absorption of nitrogenous matter from the stimulating body: a piece of indigestible matter produces less secretion and without proteolytic powers. The body of the insect, or the cube of white-of-egg, enveloped in the secretion, is slowly digested, and the dissolved material, together with the secretion itself, absorbed into the cells of the leaf. In the white-of-egg the rounding of the edges of the cube can easily be followed. All that remains of an insect when digestion is complete are the insoluble chitinous parts. The process of digestion in the Butterwort, and Venus' Fly Trap is essentially the same as in Sundew. The difference lies in the varying perfection of the mechanism.

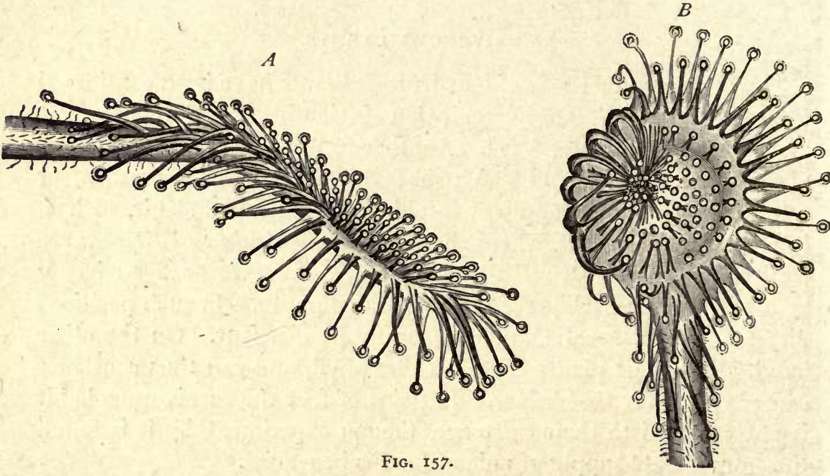


FIG. 157.
Leaves of *Drosera rotundifolia*: enlarged. *A*, in the receptive state before stimulation. *B*, after stimulation, viewed from above, with tentacles partly incurved. (After Darwin.)

In *Nepenthes* the peculiarly formed leaves are an effective trap for luring small animals into the fluid that partly fills the pendent urn (Fig. 158). In Botanic Gardens these are often choked by the partially digested remains of ants, cockroaches, and other victims. There is no motile mechanism that catches them, but only a static trap. The lip of the urn slopes inwards, and is cartilaginous and smooth, with secreting glands at its inner rim. Insects attracted by the secretion into a dangerous position on the smooth sloping surface lose their footing, and fall into the urn, from which, owing to the absence of foothold on the converging walls, there is no escape. Death and digestion follow.

The secretion within the urn is exuded by numerous large, button-shaped glands upon its inner surface. Each is covered on its upper side by a downward drooping hood, which effectually prevents its use as a step in climbing up out of the fluid. Hooker showed in 1874 that the fluid within was capable of dissolving white-of-egg. It appears that here also the absorption of some digested matter is necessary before the ferment is secreted in quantity. The ferment is of the tryptic type, for it has been shown that it is able to break down digested proteids into the state not only of peptone, but in part to the state of amide crystalline bodies. In this form they are readily absorbed by the plant, which thus receives a supply of combined nitrogen, as well as of certain mineral salts. In the somewhat similar, though morphologically quite distinct urns of *Sarracenia* and *Cephalotus*, ferments have not been demonstrated. Nor have they in the smaller traps of *Utricularia*, though glandular hairs are present on their inner surface. But this is not surprising since the urns are commonly sunk in water or in mud, and the presence of water inside them would interfere with the necessary tests.

FIG. 158.

Pitcher of *Nepenthes*, with part of the wall removed to show the fluid (*F*) secreted by the glands borne on the inner surface. (½ natural size.) (After Strasburger.)

The extraordinary forms and mechanisms thus seen in carnivorous plants seem to accentuate the importance for them of the gain which follows on this accessory nutrition. Yet all of these plants can live without it, while a surfeit of animal food may be experimentally shown to be harmful to them. These plants stand out as some of the strangest results of special adaptation, and strike the observer as showing a grotesque disproportion between the end gained and the means adopted to secure it.

Thus many plants, and often those in which we should least expect it, have other methods of nutrition than the autotrophic process. The degree of dependence upon irregular methods varies greatly. The habit is not restricted to any one family or group of plants. It has been seen that sometimes single species or genera, sometimes whole families are affected. These phenomena are chiefly found in advanced families such as Leguminosae, Orchids, Heaths, or Orobancheae, rather than in those held to be primitive. All these facts taken together lead to the conclusion that *irregular nutrition among Flowering Plants is secondary.* Its methods have been adopted individually, and comparatively late in Descent, by organisms of which the ancestry were autophytes. Moreover it has not started along any single line of Descent, but along many. In this, as in so many special adaptations, homoplasy, or parallel development is frequently illustrated. The advance has been along lines of opportunism. Close crowding has encouraged it. Use has been made of such circumstances as offered in order to achieve the end of the plants' existence. *That end is not merely the maintenance of the individual, but the propagation of the race by new germs.* The case of *Rafflesia* illustrates this in a striking though extreme manner. (Figs. 145, 146.) Its vegetative system is reduced in accordance with its parasitism, to the level of fungal hyphae. But its flower is of enormous size, complex in structure, and results in a great output of seeds, each containing a new germ (*ovula numerossisima*, as Robert Brown called them). The nutritive system though reduced, is still effective for nourishing this flower. Thus the propagation of the race takes precedence over the vegetative development. This is the ultimate lesson taught by the study of irregular nutrition, and by the morphological degradation of the vegetative system, which so often follows on its successful practice. *Propagation is the real end. Vegetative development is only a means to that end.* The whole vegetative system may be regarded as a physiological scaffold, while the mechanism of propagation is the substantive building which is erected by means of it.

CHAPTER XII.

VEGETATIVE PROPAGATION.

In the life of any organism there are two chief phases, which are not always distinct from one another, and may overlap. The one secures the maintenance of the individual, the other increases the number of individuals. Thus far the former only has been followed. It has been seen how the Plant is established on germination, and developed as an organism which can maintain itself. It is able, moreover, to acquire material in excess of its immediate needs. This is in itself a necessary condition of increase in number, for there must be at least a sufficiency of material for forming the new germ or germs. But it is not possible to put any measure on the amount of material required to be at hand before increase takes place. An unusually early propagation in a Seed-Plant is seen in the Potato, where the seedling may form a tuber from the axillary bud of each cotyledon (Fig. 159).

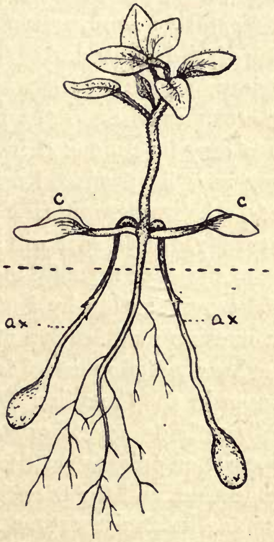


Fig. 159.
Seedling of the Potato, showing how the buds (*ax*) in axils of the cotyledons (*c*) develop as tubers. (After Percival.)

There are two methods of increase. One is by *Vegetative Propagation*, which consists simply in separation of a part of the plant-body as a being physiologically independent of the parent. During its early development that part is nourished by the parent. The separation may finally be completed by the death of the parent, as in the Potato; or it may be the result of rupture or death of the tissue connecting it with the parent, as in the bulbils of the Orange Lily. It is the separation that defines the new individual. *In origin it was a part of the parent plant, the characters of which it retains and repeats.* The process may be simply described as *budding*; or more specifically as *somatic budding*, as it involves the detachment of some part of the *soma*, or plant-body.

The other method is by *sexual reproduction*, which involves the fusion of two *sexual cells, or gametes*, to form a new cell, the *Zygote.* This is also the starting point of a new individual. The two gametes are more or less distinct from one another in origin and character. The offspring shows features derived from both of the parent gametes. But it differs in some degree from either of them. The process is not then a mere act of repetition, as the budding is. On the contrary, *Sexual Reproduction may be a source of something different from either parent, though it shares the qualities of both.*

Vegetative propagation is a very wide-spread means of increase both of wild plants and of those in cultivation, and there is considerable variety of detail in the way in which it is carried out. In Flowering Plants it consists in the independent establishment of buds. Such buds may be produced in the normal sequence, as *axillary buds*; or they may be produced out of the normal sequence, as *adventitious buds.* Examples of each will first be taken from plants growing naturally, and later it will be seen how the art of the cultivator makes use of these, or actually induces their production artificially.

The propagation by *buds formed in the normal sequence* sometimes involves no modification of the shoot, and is so simple a process that it is hardly distinguished from ordinary normal growth. An example is seen in the Canadian Water-Weed (*Elodea*). The shoot produces axillary buds which grow into long branches. Either mechanical rupture, or progressive decay from below, may sever the physiological connection, and the branch becomes a new individual. *Elodea* shows also the indefinite degree to which this vegetative propagation may extend; for since the plant was introduced about the middle of the nineteenth century, it has spread throughout the water-ways of Britain, notwithstanding that only the female plant was introduced; and, being dioecious, it does not propagate here by seed. This simplest of all methods of vegetative increase in numbers is very common. Ordinary perennials, such as Grasses and Sedges, give abundant examples of it.

In other plants some slight modification of the axillary buds may be seen, giving biological advantages. For instance, there may be an elongation of the basal internodes, leading not only to vege ative increase, but also to a wide extension of the area occupied. A "runner" is thus formed, and the bud is carried out to a distance from the parent plant. It there roots in the soil without competing with the parent. This is seen in the Strawberry (Fig. 160), the Silver-Weed, the Bugle, and many other creeping herbs. In other cases storage, either in the axis or the leaves of the bud, gives it an additional advantage at the start, especially in plants subjected to seasonal change. Such buds may be produced above ground, as in the bulbils of the Lily or

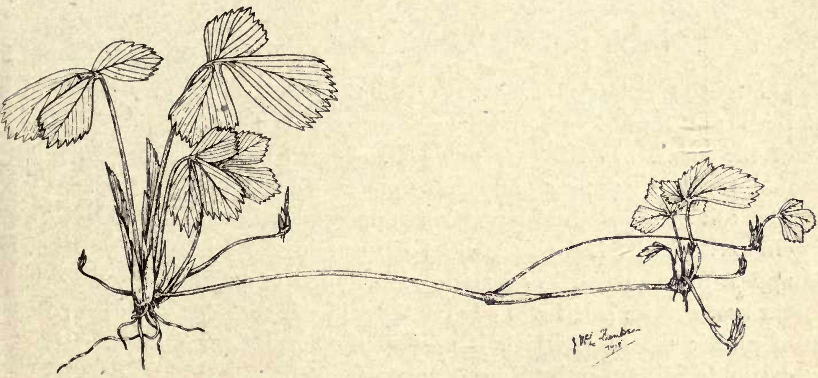


FIG. 160.
Strawberry Plant, bearing axillary buds developed as runners, with long internodes which may branch and root at their distal ends. (Reduced to ½.)

Onion; but more frequently they are buried, as in the Potato (see Fig. 138, p. 185), or Artichoke. Perennation as well as increase in numbers is secured by such measures as these. Sometimes the parent survives, as in *Saxifraga granulata*, or *Scrophularia nodosa*; in other cases it dies, as in the Potato and Jerusalem Artichoke. In the latter cases, since each tuber is borne on an elongated stalk and can grow into a new plant, both spread and increase are secured, as well as perennation. It will be unnecessary to illustrate further the manifold varieties of detail shown in vegetative propagation by means of buds produced in the normal sequence. In nature a very large proportion of individual plants may be traced as having been produced in this way. But it is more common in herbaceous than in woody plants.

Adventitious buds, that is, buds formed in positions where buds are not normally present, serve the same end, but they are less frequent.

The case most commonly quoted is that of *Bryophyllum*, one of the House-Leek family, whose fleshy leaves may be induced to form buds in the notches of the leaf-margin, by pegging them down on moist soil (Fig. 161). These buds root themselves in the soil, and as the leaf decays they remain as substantive plants. A similar casc occurs in the familiar Cuckoo Flower (*Cardamine pratensis*). In old plants the radical leaves lie along the surface of the soil, and buds are formed on the upper surface, usually at the forking of the veins. In *Malaxis paludosa*, a small native swamp Orchid, minute buds appear at the tips of the leaves. Frequently the adventitious bud-formation appears under some stress of circumstances. But this is most evident in those cases where they appear upon roots. For instance, if a Poplar or an Elm be cut down, the root-system is left still alive in the soil. It contains a large supply of plastic material, which it uses in the formation of buds. They originate without order from the region of the cambium, and rise above ground as "suckers" (Fig. 162). Fruit trees, such as plums, if severely pruned, also produce similar suckers. These are familiar objects in the vegetable garden, where plums are trained against a wall and pruned. Such adventitious developments are clearly related to a check of the aerial shoot, and may be held to be a method of recovery from it.

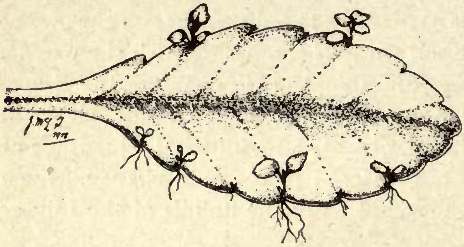


FIG. 161.
Leaf of *Bryophyllum* after culture on moist soil, with adventitious buds borne at its margins.

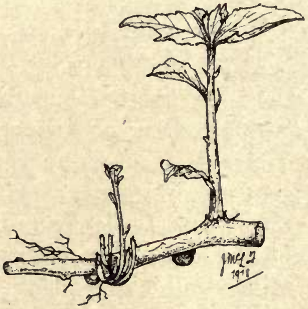


FIG. 162.
Root of *Populus alba*, bearing adventitious buds, which come above ground as suckers. (Reduced.)

A special interest attaches to the fact that vegetative propagation is common among alpine plants. In them vegetative buds easily detached replace flower buds. This is seen in *Polygonum viviparum*, where the lower part of the inflorescence bears as a rule bulbils only, while a variable number of flowers occupy its distal end. The rare *Saxifraga cernua* seldom flowers in Britain, but usually bears bulbils instead. Certain Grasses frequently show this state, *e.g. Poa alpina*, *Deschampsia caespitosa*, and particularly the mountain variety of the Sheep's Fescue (*Festuca ovina*, var. *vivipara*). Such developments may be held as a response to stress of circumstances. The short season and alpine conditions being unfavourable for flowering and fruiting so as to set seed, the formation of vegetative buds gives a greater certainty of survival. Any advantage that follows from sexual propagation is sacrificed to attain that certainty.

Such examples suggest how various are the ways in which Flowering Plants propagate by budding. It is, however, rare among Gymnosperms. In lower forms, such as Ferns, Horse-tails, and Club-mosses, it is common. Among the most prolific of all plants in this way are the Mosses, some of which are practically unknown in fruit. Finally in the Algae, and especially in the Fungi vegetative propagation is conspicuous as a source of increase. This raises the question whether this method might not suffice for all practical purposes. Cases are known among cultivated Flowering Plants where it is continued indefinitely. The cultivated Banana and the Pineapple are seedless. The Sugar Cane rarely flowers. The Jerusalem Artichoke has been grown regularly in British gardens for two centuries from tubers. There appears in fact to be no definite limit to repetition of increase by budding. It has always been favoured by horticulturalists for the good reason that the exact qualities of the strain or variety are retained, while in propagation by seed those qualities are liable to be modified or lost. *It is the weakness, as it is also the strength of somatic budding, that there is as a rule no evolutionary change, but only repetition.*

This repetition is exactly what the horticulturalist requires when dealing with special strains of cultivated plants. His methods depend on the maintenance of the desired strain through buds produced in normal sequence, or adventitiously induced. *Cuttings* and *slips* are merely parts of the shoot of the parent plant bearing one or more normal buds. They are kept under circumstances to promote root-formation, which takes place best if the cut be made just below a node. The shoots must be selected of the right age and condition to secure success. Greater certainty follows on *layering*, in which the shoot it is desired to establish is not separated from the parent, but pegged down in the soil, with or without a notch or ring, cut so as to check the downward flow of plastic material. This promotes root-formation, after which the shoot may be detached (Fig. 163). This method is used for rapid production of established plants in the case of currants, vines, and various fruiting stocks. But some plants are refractory and difficult to root. In such cases the stem below the

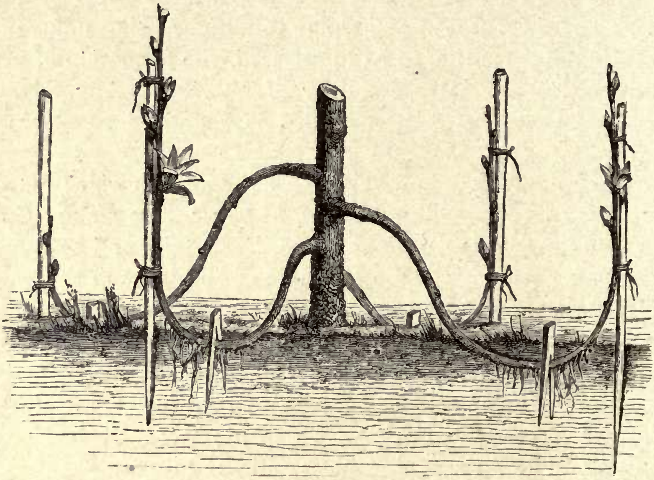


FIG. 163.
Propagation by layering. (After Figuier.)

shoot it is desired to establish may be nicked with a knife, and packed with wet moss or soil. Roots may then be formed, after which the shoot may be severed.

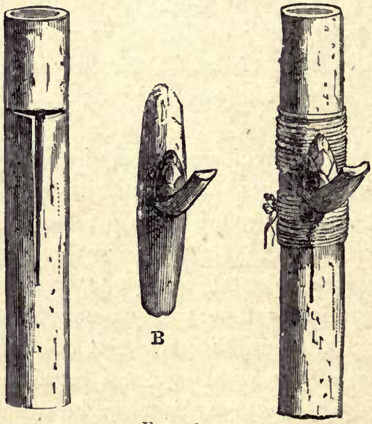


FIG. 164.
Method of shield-budding or cushion-grafting. (After Figuier.)

Budding and *grafting* are methods commonly used for woody plants, but latterly they have been employed also with success in succulent plants. These processes consist in the insertion of a single bud, or of a shoot bearing a number of buds, not in the soil, but upon the corresponding tissues of some related plant. In the case of *shield budding*, which is largely practised in the propagation of varieties of roses, a bud is removed from the plant which it is desired to propagate, together with an area of superficial tissues separated at the cambium layer. A surface for its reception is prepared by a T-shaped cut into the tissues of the stock that is to receive it, and the tissues down to the cambium are separated from the woody column (Fig. 164). The cambium-layer of the shield is placed in contact with the wood, and the whole is bound up with bast and wax to exclude air and intrusive fungi. The two living tissues form each a callus, which unites, and their junction is such that the woody column of the stock provides the transpiration stream to the

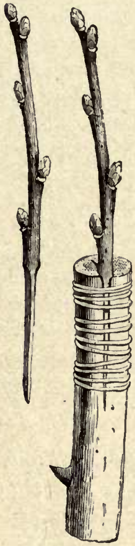


FIG. 165.
Cleft-grafting.
(After Figuier.)

FIG. 166.
Approach-grafting or inarching. (After Figuier.)

alien bud. *Grafting* is essentially the same process; but a woody shoot with a number of buds is removed, and inserted upon a correspondingly cut surface of the stock, so that both the active cambial tissues of both shall be in contact (Fig. 165). *Inarching* or *approach-grafting* is similar, but has the advantage of both plants remaining rooted till the union is complete (Fig. 166). After the bud or graft has fully united with the stock the head of the stock is removed, and the graft or bud takes its place, retaining its original qualities. But according to the vigour of the stock it may mature earlier in the season, and fruit more profusely than upon its own root. Besides such advantages, time is also saved. For it is much quicker to insert a graft or bud upon an established stock than to raise an equally strong plant from a cutting.

The graft, or bud, or *scion*, as it is often called, need not necessarily be of the same species as the stock upon which it is placed. For instance, the Peach may be grafted on a Plum stock, the Apple on the Pear, the Pear on the Quince, or the Medlar on the Hawthorn. But the affinity must be close, such as within the Natural Order. The stock often influences the scion, though the latter retains its essential characters. The size, age of coming into fruit, or the period of maturing of the fruit may be affected; but such changes are ascribed rather to the nutritional capacity of the stock than to any more profound cause. On the other hand, it has been stated that occasionally a more intimate fusion of characters of the stock and of the scion has been set up. Reputed *graft-hybrids* exist. The most notable is *Cytisus adami*, of which the parental forms are stated to have been the common yellow Laburnum and *Cytisus purpureus*, the latter having been inserted on the former. The plant which resulted has been widely propagated. It shows usually purple flowers, but certain branches "throw back" to the common yellow form. It was suggested that nuclear fusion, of a sexual nature, took place in the region of the callus of the graft, and was the source of the fusion of the characters. A recent careful examination of its nuclear details makes this explanation appear improbable. There is even historical reason as well as comparative probability for an alternative suggestion, which has met with acceptance. It is held that the plant from which the original purple graft was taken was itself not a pure species, but a hybrid; in which case the facts would follow as recorded. Thus the probability is that *Cytisus adami* is not a graft-hybrid. Better evidence will be necessary before the existence of graft-hybrids can be held as proved.

The horticulturalist also induces the formation of adventitious buds, and some plants respond freely. If a lamina of *Begonia* or of *Gloxinia* be cut transversely across the main ribs, and be cultivated in heat on damp soil, buds may be formed in relation to any cut vein. These buds root themselves in the soil as new plants. It is stated that each bud arises from a single cell of the parent leaf. (Fig. 167.) Certain Fern-rhizomes, and even the bases of their leaves behave in a similar way; but it is in the Mosses that there is the most remarkable profusion of this adventitious development from single cells of the injured part. If moss plants be chopped up into small pieces, any piece in which an uninjured cell remains may start a new vegetative growth, and lead ultimately to a new moss plant.

There are certain weeds of farm land which depend upon a somewhat similar vegetative multiplication for their survival, when the land is worked by plough and harrow. The Couch Grass (*Triticum* *repens*), and the Common Horsetail (*Equisetum arvense*) are cases in point. Any node serves to provide new buds ; and as the long underground rhizomes are broken up in preparing the soil, this does not eliminate, but tends to spread the weed.

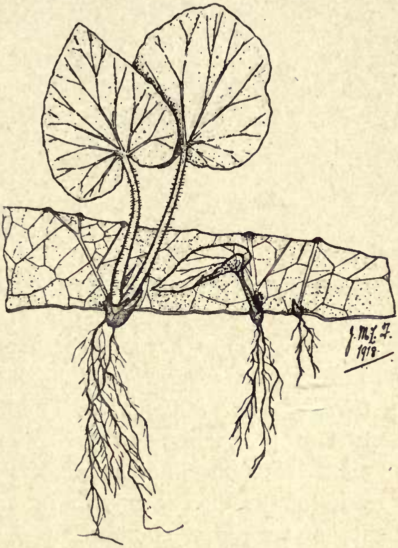


FIG. 167.
Part of leaf of *Gloxinia*, bearing adventitious buds after cultivation, in heat, on moist soil.

It thus appears that vegetative extension and propagation of the individual is a very wide-spread feature, both in Flowering Plants and in those lower in the scale. It is effective in wild life, as well as under the hand of the gardener. A very considerable proportion of the perennial plants which we see have been so produced. This applies especially to the Grasses and Sedges, whose perennial rhizomes are constantly growing forward, and as constantly rotting progressively from the base. But probably the most prominent, and at the same time familiar example of all is the Bracken Fern, which covers immense areas all over the world. Its underground rhizomes branch freely ; if a single specimen be dug up, and followed backwards, the brown region of decay is soon reached. Young seedling Brackens are rarely met with in the open. Here then is a case where the apical growth and branching of the individual are practically unlimited, and where its vegetative increase in number of physiologically independent units appears to be unlimited too. It may be held as a type of that vegetative spread and multiplication which, though it involves no special development for the purpose, is frequent among perennial plants.

CHAPTER XIII.

THE INFLORESCENCE, AND THE FLOWER.[1]

In Flowering Plants *Sexual Reproduction* is carried out in the Flower. It results in the *production of Seed.* Contained in each ripe seed is the *Germ of a new individual.* The Flower which serves this uniform purpose of producing new germs may take an infinite variety of different forms in different plants. But however various the appearance of the Flower may be in outline, or in the number or complexity of its parts, comparison shows that the organs which are directly connected with the sexual process, and the details of that process, are in all cases essentially the same. This suggests that *the differences are accessory, and that the propagative process itself is the real end.*

The Flower.

The Flower is found to consist of parts which fall into certain definite groups, or kinds of organs. But they may vary greatly in number, while all the kinds of organs need not be represented in the same flower. Some like the Water-Lily, or the Rose or Quince, consist of numerous parts representing all the kinds of organs (Fig. 168). In other cases the flower in the strict sense may comprise only a few parts, or in extreme cases only a single one of them, as in the Spurge (Fig. 169). There is in all cases a prolongation of the stalk to bear the floral parts; but it terminates abruptly, and is usually more or less widened out laterally, so that the appendages can be closely crowded upon it. This is called the *floral receptacle*, and since its apical growth stops, the result is that the flower is always distal, that is, it is borne at the end of its stalk. The parts which the receptacle bears may be grouped as:

[1] This chapter will be best understood after a number of the types of Floral Construction described in Appendix A have been dissected and examined.

(1) *Sepals*, which are the lowest and outermost parts. They are usually leaf-like, being firm and green in texture. They constitute the *Calyx*, the office of which is protective to the inner parts of the young bud (Fig. 168, *Sep.*).

(2) *Petals*, which lie internally to them, and are usually delicate in texture and in tint. They constitute the *Corolla*, and serve chiefly for attracting attention by colour and scent (Fig. 168, *Pet.*).

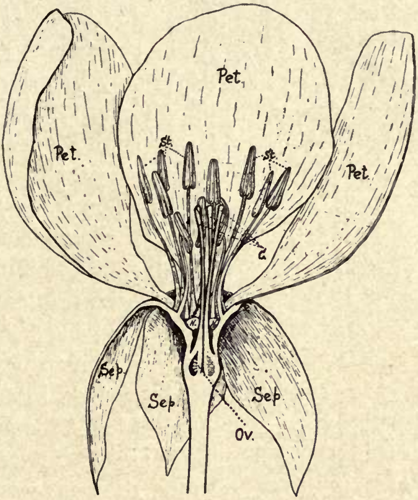


FIG. 168.

Vertical section through a flower of the Quince, *Cydonia* (*Rosaceae*). *sep*=sepals. *pet*=petals. *st*=stamens. *c*=apices of the carpels, elongated into styles. *ov*=ovules. *n*=nectaries. The receptacle is here hollowed out, so that the carpels appear sunk down into a cavity. (After Church.)

(3) *Stamens*, which are inserted internally to the petals, and are usually club-shaped, and yellow in colour. Each bears *Pollen-Sacs*, commonly four in number. The stamens are styled collectively the *Androecium*,[1] and their function is to produce *Pollen* (Fig. 168, *St.*).

(4) *Carpels*, one or more of which occupy the centre, and are usually of pod-like form, and either green or colourless (Fig. 168, *c*). They are styled collectively the *Pistil*, or *Gynoecium*,[1] and their functions are

[1] The correct spellings of these words, as based on derivation are *androecium* and *gynaeceum*. But as it is inconvenient to maintain this difference in spelling in view of the cognate meanings of the terms, it is best to sacrifice strict accuracy, and to assimilate the spellings. The words will therefore stand in the text as *androecium* and *gynoecium*.

to receive the pollen, and to enclose and protect the *Ovules.* (Fig. 168, *ov.*) Under favourable conditions each ovule is able to produce a single new *germ,* and to develop into a mature *Seed.*

The relations of these floral parts to the receptacle are similar to those of the foliage leaves to the stem; for they arise laterally upon it, and their succession is such that the oldest are the lowest, or outermost, and the youngest the innermost, or nearest to the tip. *No buds are produced in their axils.* As in the foliage shoot the appendages may be arranged spirally, or in whorls, but in the flower the latter is the more common. The members of the successive whorls usually alternate with one another. This is convenient for their close packing in the bud. The parts of the flower are as a rule closely aggregated together, while those of the vegetative shoot may be separated by long internodes. But all normal leafy shoots terminate in a bud, and so, at least in the young state, the two are alike in this also. *There are thus marked analogies between the foliage shoot and the flower. Both are constructed on the same plan. There is, however, one absolutely distinctive character which separates them. It is the presence in the Flower of the Organs of Propagation, called Sporangia.* These have no correlative in the vegetative region. They are organs of a separate category altogether. *Accordingly the Flower may be defined as a simple Shoot which bears Sporangia.*

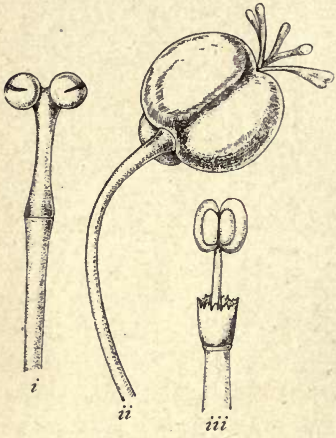


FIG. 169.

(i.) Single male flower of Spurge (*Euphorbia*), consisting of one stamen, with abortive perianth. (ii.) Single female flower, consisting of three carpels, and an abortive perianth. (iii.) Single male flower of *Anthostema* (Euphorbiaceae).

In the Flowering Plants the *Sporangia are of two sorts,* viz. *Pollen-Sacs* and *Ovules.* In very many cases these are both present in the same flower, which is then called *Hermaphrodite.* But in others only one or the other is present. When the flower contains stamens bearing pollen-sacs, but no carpels, it is described as *Staminate*; when it has carpels bearing ovules, but no stamens, it is called *Pistillate.* The biological importance of these differences of distribution is great, as they are closely related to the mechanism of intercrossing.

The two types of sporangia, viz. pollen-sacs and ovules, and the parts that bear them, viz. the stamens and carpels, are often described as organs of sex, and flowers in which only one or the other occur are called "male" or "female." It is better to call them staminate and pistillate. All the old terminology of the flower has been based upon a misconception. It should be clearly understood that there has been an error of description. It is almost impossible to eradicate that error without discarding much of the current terminology, which it is hardly necessary to do provided that the difficulty is clearly understood. The early writers suffered from an imperfect knowledge of fact, and a want of proper comparisons. For our present purpose those comparisons cannot be made intelligible till certain plants lower in the scale have been examined. At the moment the conclusion must be stated without the detailed grounds for it. It must suffice to say here that *the sporangia of the Higher Plants produce spores (pollen-grains, and embryo-sacs), and it is from these that the actual sexual organs originate. But neither stamens nor carpels, nor pollen-sacs nor ovules, are themselves organs of sex. They are all parts of the neutral plant, specialised in relation to the sexual organs which it is their ultimate function to produce.*

The Inflorescence.

The *Flower* defined as above is usually marked off from the vegetative system that bears it as a definite unit. When borne singly, as in the Tulip or Buttercup, no one has any doubt what is meant by the term. But such units are often borne in large numbers together upon a *common branch-system, or Inflorescence*, as in the trusses of a Horse-Chestnut, or a Lilac; and sometimes the flowers of an inflorescence are so closely packed together that the whole may be mistaken for a single flower, as in the Daisy. It is thus necessary to analyse the branch-systems that bear the individual flowers.

The *Inflorescence* often presents marked features, and as these recur in related forms they have their value in classification. The methods of branching in an inflorescence, which are often very complicated, are the same as those found in the vegetative region. Here as there *axillary branching prevails.* The leaf, in the axil of which a flower bud arises, is usually small and simple by reduction; sometimes it is abortive. These reduced leaves are termed *Bracts.* Where they are borne upon axes of relatively higher order they are commonly smaller, and are styled *Bracteoles.* But there is no real difference, except in their relation in the branch-system. The bracts serve to protect the buds while young. The production of many flowers together, so as to form a conspicuous group, even though the flowers may be individually small, brings advantages in mutual protection; but still more in relation to the transfer of the pollen. In particular, a complicated branching not only gives the opportunity for a larger output of seeds, but it may also provide a succession of flowers which bloom during a prolonged period, instead of simultaneously. These are among the biological advantages gained by complicated inflorescences.

The characteristic features which inflorescences show depend upon four main factors: (i) the arrangement of the leaves (bracts) in the axils of which the branches arise; (ii) the proportion of intercalary growth of the several axes; (iii) the number of flower-buds produced; and (iv) the succession in which the buds mature. Of these the most important is the last, and inflorescences may be classed according to its consequences as *Definite* or *Indefinite*. If a distal flower blooms first that will stop the apical growth

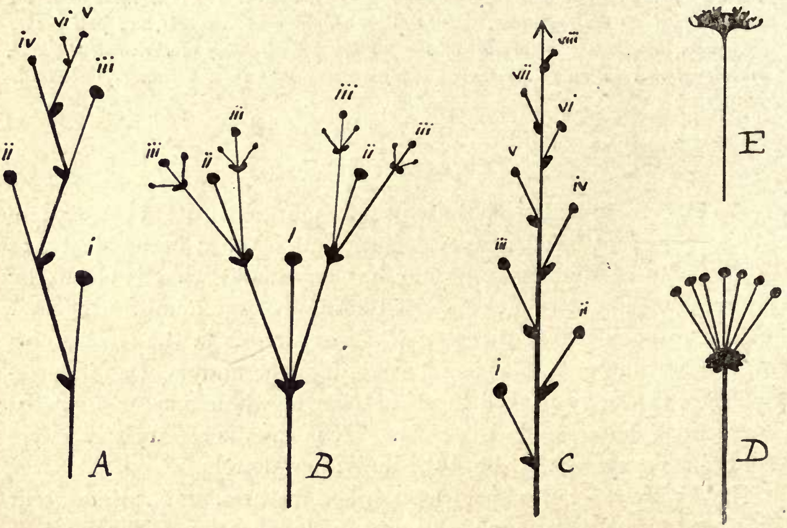


Fig. 170.
Diagrams of common types of Inflorescence. *A*, *B*, definite; *C*, *D*, *E*, indefinite. The numbers indicate the succession of the flowers. See text.

of the main axis, and all further flowers must be borne on lateral axes. Such inflorescences are termed *Definite*, or *Cymose* (Fig. 170, *A*, *B*). They commonly develop *sympodially*, that is, the lateral axes grow so as to overtop the main axis. But if the buds on lateral branches bloom first, the apex may still continue to grow, and to form additional bracts and flowering buds. Such inflorescences are called *Indefinite*, or *Racemose* (Fig. 170, *C*, *D*, *E*). They usually work out along *monopodial* lines, that is, the main axis remains dominant, and the lateral axes are accessory.

The simplest *Cymose* or *Definite* inflorescence is illustrated by the Tulip, with its solitary flower terminal on the *peduncle*, or main flower-stalk. But in the bulb below, an axillary bud matures during the season, which will repeat the flowering axis in the next year, and so on. The Tulip is then a definite inflorescence, with an interval of a year between its flowers. Its branch-system is sympodial, each succeeding axis overtopping its predecessor.

The Buttercup shows a similar condition, but its sympodial character appears in the flowering shoots of the single season. (Fig. 170, *A*.) In these cases the leaves are alternate, so that each lateral branch is solitary. But if the leaves which serve as bracts in a cymose inflorescence are opposite, as they commonly are in the Pink Family, and in many Gentians, the main axis will bear two lateral branches at the same level. (Fig. 170, *B*.) The result is

FIG. 171.
Inflorescence of Centaury: a dichasium. (After Figuier.)

FIG. 172.
Inflorescence of Verbena; a spike. (After Figuier.)

what is called a *Dichasium* (Fig. 171). The difference depends here upon the leaf-arrangement, but the method is the same as before; and a number of sympodia are the result, instead of only one. Various other Cymose inflorescences are built up on fundamentally the same principle, but differing in the orientation and succession of the bracts, and consequently of their individual flowering branches, or *pedicels*. Examples are seen in the common Rock Rose, and in *Echeveria*.

The simplest *Racemose*, or *Indefinite* inflorescence is the *Spike*, where flowers in an acropetal sequence are seated directly in the axils of the bracts borne by the main axis or *peduncle*, as in *Verbena* (Fig. 172). Or the lateral flower-stalks (*pedicels*) may be elongated, giving the condition of the typical *Raceme*, as in the Currant (Fig. 173). Or again the pedicels may be themselves branched, as in the Vine, giving the *panicle* (Fig. 174). Such differences depend partly upon differences of intercalary growth, partly upon branching of a higher order. In all of them the distal buds develop latest. It happens, however, not uncommonly that the characters may be mixed. For instance, a cymose tendency may appear in the higher branchings of a panicle ; as is well seen in the inflorescences of Figwort, where the terminal flower of the lateral branches blooms before those seated below.

FIG. 173.
Inflorescence of Currant : a raceme. (After Figuier.)

The racemose type is particularly subject to extreme differences of growth in length. The result is seen in certain inflorescences which characterise large families. The most important are the *Umbel* and the *Capitulum*. Both result from suppression of growth in length. If the axis be abbreviated in the part that bears the pedicels these will all appear to originate from the same level, giving a candelabrum-like branching, called a *simple Umbel* (Fig. 170, *D*). The subtending bracts are also grouped into a close investment just below the group of branches. It is called collectively an *involucre*, and serves for protection in the young state (Fig. 175). The branching may be repeated in each of the pedicels, each being provided with a *partial involucre* of bracts. The result is the *Compound Umbel* (Fig. 176). But as in other complicated inflorescences, the bracts of the partial, and even the general involucre, are liable to be reduced, or entirely absent. The closely grouped buds protect one another while young, so that the bracts become superfluous, and are liable to be suppressed. Such inflorescences are characteristic of the Umbelliferae ; but various degrees of abbreviation of the axes are found in other families, giving rise to modifications of the raceme or panicle sometimes described as corymbose.

If, however, intercalary growth be reduced both in the peduncle and the pedicels, all the flowers will appear aggregated in a dense head. The axis of the whole inflorescence is then usually enlarged into a *general receptacle*, upon which numerous flowers are seated. Such an inflorescence is called a *Capitulum* (Fig. 170, *E*). It is characteristic of the Compositae. Here again

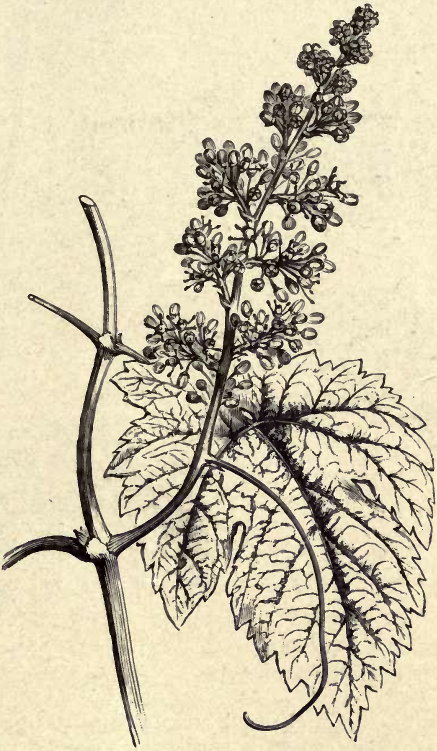


Fig. 174.
Inflorescence of the Vine: a panicle. (After Figuier.)

the bracts form a general involucre protecting the whole head, while a bracteole normally subtends each flower borne on the receptacle (Fig. 177). But as these are closely packed, they must mutually protect one another. The bracteoles are then superfluous, and are often absent, as they are in the Oxeye Daisy and the Dandelion (Fig. 234, p. 290). Similar capitula are found in the Sheep's Bit (*Jasione*) among the Campanulaceae, and in the Teasel and Scabious among the Dipsaceae. It is in fact a character recurrent in several distinct families, though it finds its headquarters in the Compositae. Its biological effect is that an inflorescence acts functionally in the same way as a single flower.

Inflorescences usually develop on a *radial* plan, especially those of indefinite type. But many definite inflorescences appear distinctly *dorsiventral*. These

FIG. 175.
Inflorescence of *Astrantia*: a simple umbel. (After Figuier.)

FIG. 176.
Inflorescence of Chervil; a compound umbel. (After Figuier.)

are so arranged that each flower as it blooms is directed upwards, thus securing prominence at the time of pollination. This is seen in the Forget-me-nots

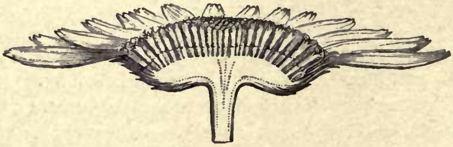


FIG. 177.
Inflorescence of Daisy: a capitulum. (After Figuier.)

and Rock-Roses. In the Grasses, which are racemose, even upright inflorescences may be dorsiventral. This is seen in the Cock's-foot (*Dactylis*) and the Mat-weed (*Nardus*).

METHODS OF COMPARISON OF FLOWERS.

No attempt will be made here to describe fully the wide range of difference in construction of Flowers, nor to treat those differences systematically, as a basis for a natural grouping into Families. Such details will be left over to Appendix A. It must suffice to illustrate the *methods* by which such comparisons are most easily presented, and to state the *leading factors* upon which these differences depend. Certain essential facts of floral construction may be obtained from a median vertical section (Fig. 168, p. 221). This will give the form and proportion of the receptacle, and the relative levels of the successive organs which it bears. But it cannot indicate their number, or their position relative one to another. These facts may be obtained by observation from above, and be plotted into a *floral diagram* (Fig. 178). This allows of the representation of each constituent part. It also gives the orientation of the flower relative to the axis and subtending bract. The side next the axis is described as *posterior*, that towards the bract *anterior*. The plane including the axis and the midrib of the bract is called the *median plane*; that at right angles to it the *transverse plane*. It is thus possible to plot the constituent parts in ground plan, and to show their relation to these planes. But the floral diagram gives no record of the elevation. Accordingly it must be used in conjunction with vertical sections in order to complete the study. A compact mode of registering both is found in the *floral formula*. If S represents the Sepals, P the Petals, A the Androecium, and G the Gynoecium, the number of parts of each may be added as a numeral (∞ indicates an indefinite number). Where the Calyx and Corolla are not differentiated, P may stand for Perianth. Where the parts of one category form more than one whorl, this may be shown by giving a separate figure for each. The mutual relations of the parts can be indicated by brackets, thus showing where parts are united. The position of the outer parts relative to the gynoecium is suggested by a line above or below the latter. Other details are sometimes introduced into floral formulae,

FIG. 178.
Floral diagram of Liliaceous Flower. (After Eichler.) The small circle above represents the axis; the bract is shown below, black.

but it is best not to overload them. As examples the following formulae for common flowers may be given:

Lily, P_{3+3}, A_{3+3}, $G(\underline{3})$. (Compare Fig. 178.)
Buttercup, S_5, P_5, $A\,\infty$, $G\,\underline{\infty}$.
Myrrhis, S_5, P_5, A_5, $G\,\overline{(2)}$.
Primrose, (S_5), $\underbrace{(P_5), A_{0+5}}$, $G\,(\underline{5})$.

[For details which will explain these formulae see Appendix A.]

Factors leading to Differences of Floral Construction.

The leading factors will now be stated and discussed upon which the differences of floral construction chiefly depend. They are these:
(i) *The arrangement of the parts upon the receptacle* may be either *spiral*, as in *Adonis* (Fig. 179); or *cyclic*, as in *Ornithogalum* (Fig. 178);

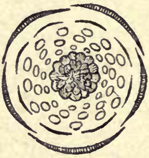


Fig. 179.
Floral diagram of *Adonis* (From Strasburger.)

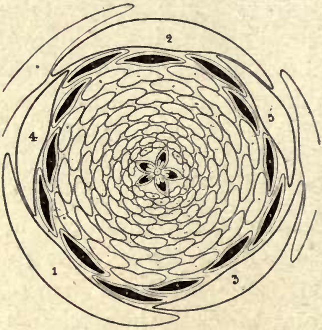


Fig. 180.
Floral diagram of *Helleborus*. (After Church.)

or an intermediate condition (*hemicyclic*) may be found between them, as in some of the Buttercup Family (Fig. 180). The cyclic type is however prevalent, especially in highly organised flowers. Since the spiral is characteristic of many primitive flowers and these graduate into cyclic types, the facts suggest that the cyclic state may often have been derivative in Descent. *The parts of successive whorls* or even in spirals also, *alternate as a normal rule.* This allows of their close packing in the bud. *They are formed in acropetal succession.* Occasionally it is otherwise, but the most prominent exceptions occur where an organ is reduced, as in the calyx of the Compositae.

(ii) *Meristic differences.* The number of parts in each successive category may differ in different flowers, and these are called meristic differences. In spiral types the numbers are relatively large and indefinite (Fig. 180); in cyclic types they are smaller, and usually definite (Fig. 178). Where the whorls are well defined the actual numbers of parts in each may be compared, and are found to vary in different flowers. Some *fundamental number*, commonly three, four, or five, then rules in the construction of each flower. Such flowers may be described as trimerous, tetramerous, or pentamerous respectively. But the fundamental number rarely holds through all the whorls, though the Flax is an example of this (S_5, P_5, A_5, G_5). Usually the androecium shows larger, and the gynoecium smaller numbers than the sepals or petals.

Not only are meristic differences common between different families, genera, or species, but even between different flowers of the same inflorescence. As regards families, the Crassulaceae show meristic variation in high degree, the fundamental figure rising in the House-leek to as many as twenty, whereas in *Sedum* it is commonly five. Within the family of the Liliaceae *Maianthemum* has 2-merous flowers, most Liliaceae have 3-merous, but *Paris* has 4-merous, or even 5-merous flowers. Within the Primulaceae *Glaux* sometimes has 4-merous, *Primula* 5-merous, and *Lysimachia* 6-merous flowers, and others have still higher numbers. Within the genus, *Gentiana campestris* has 4-merous, and *G. amarella* 5-merous flowers, while species of *Saxifraga* may show flowers 5-, 6-, or 7-merous. In the same inflorescence *Adoxa* and *Ruta* both show meristic variation. In *Ruta* the terminal flower is 5-merous, and the lateral flowers 4-merous. In *Adoxa*, as a rule, the terminal flower is 4-merous, and the lateral flowers 5-merous. Such facts are a warning against any undue faith in numbers of parts as themselves indicative of affinity.

(iii) *Fusion of Parts.* In some simple flowers like the Buttercup all the floral parts are *separate, or free* from one another. This state is probably primitive, and corresponds to the condition seen in most vegetative buds. But in many flowers certain parts are found to be *fused together* in the mature state. There is a real continuity of tissue between them. A familiar instance is the Primrose, where the corolla can be pulled away in one piece, though its margin clearly shows five petaline lobes. Further, if the corolla of the Primrose be opened out, five stamens will be seen attached to the inner surface of its tube. So not only is there a *cohesion* of the five petals to form a tubular corolla, but also an *adhesion* of the stamens to it. *COHESION of parts of the same category (such as petals with petals), and ADHESION of parts of different category (such as stamens to petals), are common in* *flowers, and may be held as secondary modifications of their free condition, as seen in the primitive state.*

This view is borne out by the study of development. For where the parts are fused in the mature state, they still originate as separate papillae of tissue from the growing point of the flower, just as the foliage leaves usually do. It is later that the growth extends from the individual bases of these papillae into the region between them. Consequently when mature they appear as though borne up on a common base. This is well shown in the flower of the Compositae, in which there is cohesion of the petals to form the tube of the corolla, and adhesion of the stamens to the inner surface of that tube. Fig. 188, p. 239, (v) and (vi) show how that adhesion arises. In (v) the stamens and petals are independently inserted on the hollowed receptacle; but the line where basal growth will take place is indicated. In (vi) the result is seen; for they are there borne up on a common base, which has been the result of that growth.

(iv) *Pleiomery.* By this is meant that the number of parts of one category is greater than the fundamental number for the whole flower. It is most frequently seen in the androecium, so that the stamens are in excess of the other parts. It may be a question exactly how this comes about in each individual example. *Branching or fission* of original y single parts may account for some cases; *interpolation* of additional parts, where there is room for them on the receptacle, may explain others. The distinction between these is not always clear; it turns upon comparison, and the observation of details of development. The essential feature is, however, that *more parts of one category are produced than the other whorls of the flower would give reason to expect.*

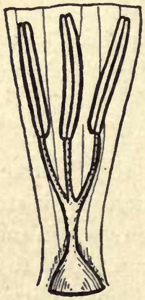


FIG. 181.
Group of three stamens of *Vellozia,* taking the place of one stamen in the normal Liliaceous flower. (After Eichler.)

Fission is most easily recognised where two or more stamens stand side by side in the place normally occupied by one; it then sometimes happens that they arise from a common stalk. The case of *Vellozia* (Fig. 181) gives a good example. *Interpolation* of extra parts may give very similar results. Sometimes it is *individual parts,* sometimes *additional whorls* that are added. All these methods appear exemplified in the Rosaceae. The following diagrams may be quoted as illustrating the pleiomeric variations within that family, though without suggesting any actual line of Descent (Fig. 182). In *Sibbaldia,* the pentamerous flower has five stamens. *Quillaija* has two whorls of five (diplostemonous), and this probably represents the fundamental type for the Rosaceae, as it corresponds to that of related families with the formula (S_5, P_5, A_{5+5}, G_5). But in the Rosaceae the matter does not stop there. Further steps are taken till an indefinite number of stamens is arrived at For instance, in *Agrimonia odorata* there is an outer whorl of five and an inner of ten (II.). In *Potentilla* there may be two whorls of ten stamens each (III.); in *Mespilus* there may be four whorls of ten each; while in *Rubus* (IV.), taking account only of the two outermost whorls, that next to the pentamerous corolla consists of ten stamens, but it is followed by numerous stamens disposed in irregular groups varying from one to four; those groups alternate with the stamens of the outer whorl. This points to an irregular interpolation of extra stameus. Such comparisons suggest that in the Rosaceae three sources of pleiomery of stamens have

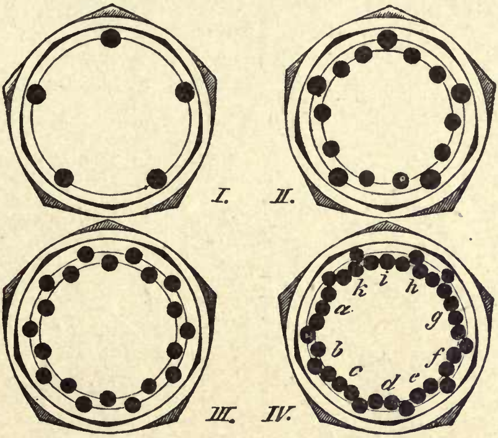


FIG. 182.

Floral diagrams of various Rosaceae (carpels omitted). I. *Sibbaldia cuneata*, and some species of *Agrimonia*. II. *Agrimonia odorata*: the first whorl of five stamens is followed by one of ten. III. *Potentilla*: the pentamerous corolla is succeeded by a whorl of ten stamens, alternating with ten stamens of the second whorl. IV. *Rubus idaeus* (special case. The pentamerous corolla is followed by a whorl of ten stamens, and from one to four stamens according to the growth of the zone of the floral axis are interpolated in the intervals between each pair of the first stamens, not only one as in III. There are three at *a*: one at *b*: three at *c*: two at *d*: two at *e*: two at *f*: four at *g*: two at *h*: three at *i*: two at *k*. (After Goebel.)

occurred, (i) fission, (ii) interpolation of individual stamens, and (iii) interpolation of extra whorls of stamens.

The *diplostemonous state*, where the stamens are twice as many as the petals, is common in those Dicotyledons and Monocotyledons which have cyclic flowers. Many polypetalous Dicotyledons show it, but with slight modification of position of the stamens, which suggest that it may have originated in different ways. It is represented also in the Gamopetalous Dicotyledons, which are divided into Tetracyclicae which have only one whorl of stamens, and Pentacyclicae which have two; making in all five cycles of floral parts. The Pentacyclic type is prevalent also in the Monocotyledons, as shown by the Liliaceous type of flower, with its many derivatives. The biological meaning of such facts is to be found in the larger supply of pollen thus provided to meet the risks of failure in pollination.

In "*doubled*" *flowers* similar features of pleiomery are seen. "Doubling" often consists merely in a petaloid development of stamens; and it most commonly occurs in flowers with an indefinite number of stamens. But it often involves also an actual increase in number of the petaloid parts, effected by methods of fission, as well as of interpolation of extra whorls, or of extra individual parts.

(v) By *Meiomery* is meant that the number of parts of one category stands below the fundamental number for the whole flower. It is

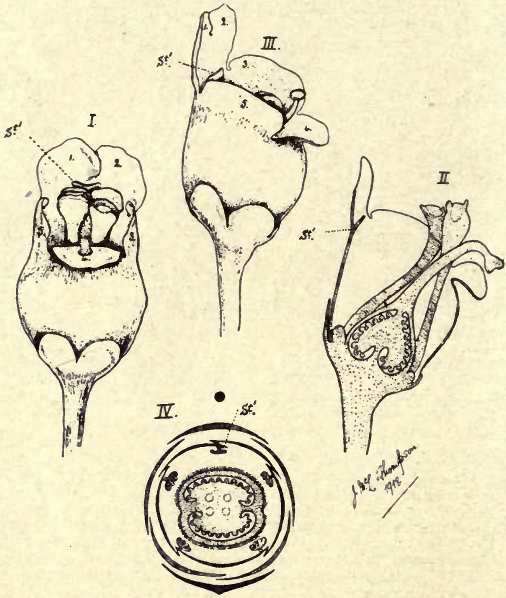


FIG. 183.
Flower of *Scrophularia nodosa*, which is pentamerous. The five stamens are represented, but the posterior stamen (*st'*) has no anther: it is merely a vestigial staminode which marks the place of a normal stamen.

most often seen in the gynoecium; but it appears also in the androecium, especially in flowers where the mechanism is highly specialised. It occurs less frequently in the outer floral parts. In the gynoecium it may be referred to a fading out of the activity of the floral shoot, or even a deficiency of room for the full number of parts. The result is that the carpels are frequently fewer than the other parts. For instance, in the Compositae, the Umbelliferae, and most Gamopetals there are only two carpels in the pentamerous flower. But in many cases it is clear that the smaller number is the result of *abortion* of parts which comparison with allied plants would show as actually present. Sometimes those parts are represented by *vestigial remains*, marking the position which those parts should hold, though they do not come to functional maturity. A good case of a vestigial stamen (*st.*) is seen in *Scrophularia* (Fig. 183).

Meiomery may appear in any of the floral parts; often it is seen in several of them in the same flower. A complete whorl may be absent: for instance the *corolla* in the Pearl-Wort (*Sagina apetala*) in the Pink Family, or *Glaux* among the Primroses: or one of the whorls of stamens may be absent, as in the Primrose. The most marked examples in the *androecium* are related to increasing precision of the floral mechanism. For instance in the Orchidaceae, derived

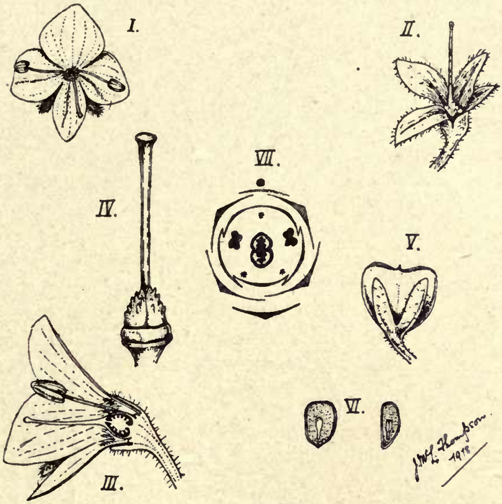


FIG. 183 *bis*.

from an Amaryllidaceous type with six stamens, *Anastasia* has three, *Cypripedium* two, and *Orchis* only one—the anterior stamen. Ginger has also only one, but it is the posterior. All of these are highly specialised types: their meiomery by abortion has followed parallel, but quite distinct lines. The Valerianaceae show various degrees of abortion of the stamens; but they also have a reduced gynoecium. Here also three loculi are present in the ovary, but only one bears a fertile ovule. The same is the case in the Oak; also in the Coco-Nut. Here the three depressed scars on the shell indicate the three carpels, but only the one that can be pierced by a pin matures its seed, and forms a germ.

A beautiful case of meiomery, involving several steps, is seen in the Scrophulariaceae. The flower is typically pentamerous, but it becomes reduced to apparent tetramery. In the Mullein (*Verbascum*) the formula is S_5, P_5, A_5, G_2. But in *Scrophularia* the posterior stamen is represented by a non-functional staminode (Fig. 183), while in others of the family it may be absent. In *Veronica* the two anterior stamens are also abortive. The two posterior petals fuse so that the corolla appears to be four-lobed; the posterior sepal, which is present in the Mullein, is represented in some species of *Veronica* by a sepal smaller than the rest; in other species it is absent, as in *Veronica chamaedrys* and the most of the Rhinantheae. Thus the flower, though typically pentamerous, has by stages of meiomery

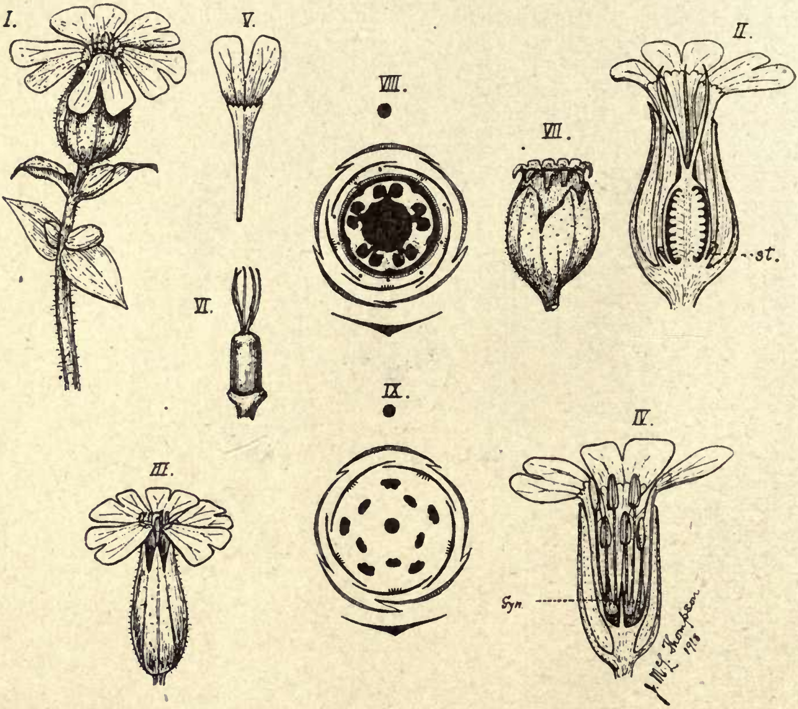


FIG. 184.
Dissections of flowers of *Lychnis dioica*. I., II., VIII., the pistillate flower in which the stamens are represented only by staminodes (*st*). III., IV., IX., the pistillate flowers in which the gynoecium is represented only by a vestigium (*gyn*).

become apparently tetramerous. Similar changes occur in the Plantains and Teasels.

Such examples serve to show that meiomery by abortion may affect any of the series of parts, and not unfrequently more than one of them in the same flower. It is probably the cause of greater divergence of detail in flowers than any other factor.

The most important cases are, however, those where one or other of the essential organs may be wholly abortive. It frequently occurs that flowers typically hermaphrodite may be *staminate or pistillate, by* *abortion* of one or other of the essential parts. A good example is seen in *Lychnis dioica* (Fig. 184). The Pink family to which it belongs have usually hermaphrodite flowers; but here the species is dioecious, which means that some plants have only staminate others only pistillate flowers. An examination of each of them shows that in the staminate flowers an abortive gynoecium occupies the centre (iv.); in the pistillate flowers ten staminodes, or abortive stamens, surround the base of the ovary (ii.). Since these parts correspond in position to the parts normally present in allied plants, they indicate that *L. dioica* is dioecious by abortion. There is evidence that this form of meiogeny has been of frequent occurrence in the evolution of Flowering Plants.

Such results are sometimes seen in extreme form, and nowhere better than in the Spurge. Comparison indicates that the Euphorbiaceae are related to the Geranium Family, which are typically hermaphrodite. Some of the Spurge Family (*e.g. Andrachne, Phyllanthus*) have calyx and corolla represented, but only stamens or carpels, never both. Others show steps of further reduction of floral structure, till in *Euphorbia* itself the staminate and pistillate flowers reach a very simple condition. The former appear as a single stamen, with a ring half way up its stalk. This represents the abortive perianth. The pistillate flower consists of three coherent carpels, with a rim below, which represents again the abortive perianth (Fig. 169, p. 222). The facts justify the conclusion that there is here a very advanced state of meiomery. Such extreme reduction is usually connected with a close crowding of numerous flowers in an aggregated inflorescence.

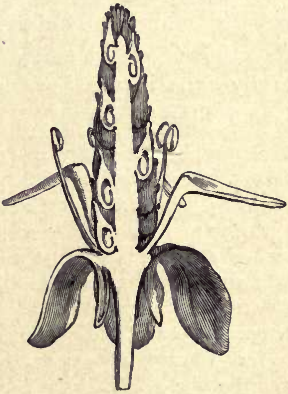


Fig. 185.
Vertical section of flower of *Myosurus*, as an example of an hypogynous flower. (After Figuier.)

(vi) *Various development of the floral axis or receptacle* accounts for very considerable differences of floral construction. As a rule the parts of the flower are closely packed upon the shortened and distended axis. In primitive types, such as the Buttercup, or Mousetail (Fig. 185), the receptacle is conical, and the sepals, petals, stamens and carpels succeed one another upon it without any interval. Where the stamens are thus seated below the carpels the condition is described as *hypogynous*, and the *ovary superior*. Occasionally in such types the axis may be elongated, so that there is an interval between the series of parts. In the Passion Flower the stamens and carpels are thus carried up a considerable distance above the sepals and petals. In the Caper Family the carpels alone are raised thus on an elongated axis. More frequently there may be a local widening out of the receptacle, in the form of a ring or cup, by growth of tissue beneath the insertion of the lower parts. The sepals, petals, and stamens may together be carried outwards upon its margin, while the gynoecium occupies the centre of the cup. This occurs frequently in certain families, and is well seen in the Rosaceae (Fig. 186, Peach). Occasionally an isolated genus shows it, as in *Subularia*, among the hypogynous Cruciferae. It may be regarded as a local modification of the hypogynous state, and is described as *perigynous*.

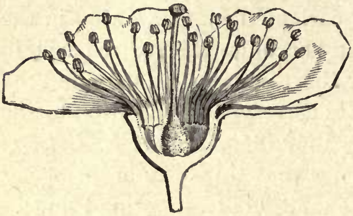


FIG. 186.
Vertical section of flower of the Peach, as an example of a perigynous flower. (After Figuier.)

A more important modification is that which leads to the sinking of the gynoecium downwards into the tissue of the abbreviated axis. This gives the *epigynous* condition, with so-called *inferior ovary* (Fig. 187, Fuchsia). The way in which this comes about is best illustrated by observing the development of a flower of an epigynous type, as may be easily done in the Sunflower or others of the Compositae (Fig. 188).

FIG. 187.
Vertical section of flower of the Fuchsia, as an example of an epigynous flower. (After Figuier.)

If median sections be cut of a young head of Sunflower, the general receptacle will be seen to bear flowers of different ages, the oldest at the outside and the youngest nearest the centre. Each arises in the axil of a bract, and the youngest may have the form of a simple convex papilla (i.). But as the growth at the centre is slower than at the periphery, the flower becomes first flattened and then hollowed. Five rounded bosses appear on the margin of cup, which are the five *petals* (ii.). The hollow surrounded by them deepens, and five other bosses appear internally to, and alternating with them. These are the *stamens* (iii.). By their formation the hollow is narrowed, and presently from its shoulders two other upgrowths are formed. These are the *carpels* (iv.). Meanwhile two small outgrowths may be seen at the outside, which previously was smooth. These are two teeth representing the *reduced calyx*, which thus appears delayed out of the normal succession. The carpels are in contact above, and enclose a cavity, which is the ovarian cavity, and the organic apex of the flower lies at the bottom of it (v.). It is here that the single *ovule* arises (vi.) and thus the ovary containing it lies apparently below the other parts. It is described as *inferior*, and the flower as *epigynous*. But it is clear that the succession of parts, excepting the

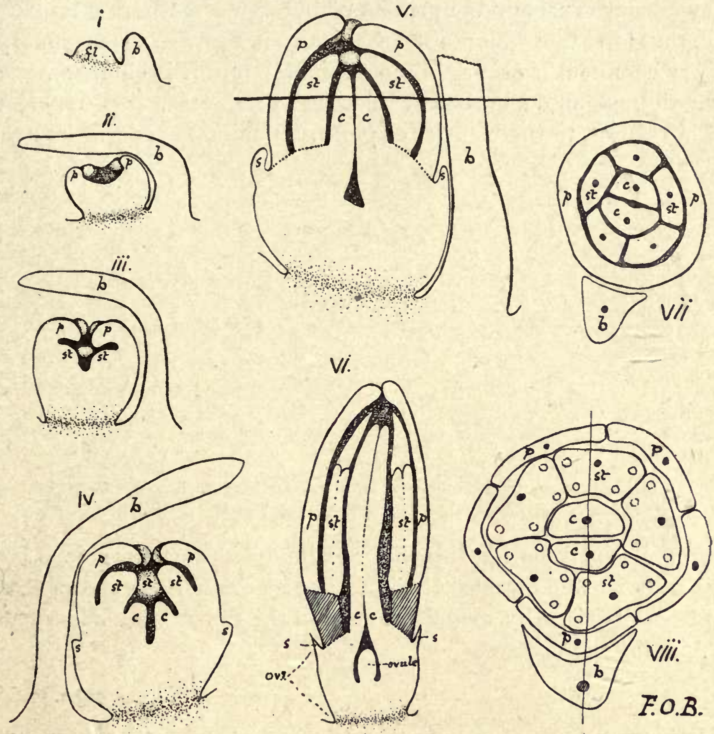


FIG. 188.

i.-viii. Successive stages in the development of the individual flower of the Sunflower; i.-vi. in vertical, vii., viii., in transverse section. *fl*=flower. *b*=bracteole. *p*=petal. *st*=stamen. *c*=carpel. *s*=sepal. (i.-v., vii. and viii. × 60. vi. × 16.) The shaded zone in vi. is the result of intercalary growth originating at the dotted line in v.

reduced calyx, is acropetal, and the carpels are actually nearest to the apex. *Thus the epigynous state results from the relatively slow growth of the apex, which is overtopped by the stronger growth around it.*

(vii) *Differences of Symmetry.* In many flowers, such as the Buttercup, Rose, or Tulip, the parts may develop equally on all sides of the axis, giving a *radial or actinomorphic symmetry.* This is believed to be a primitive condition, and it is found in flowers which are not highly specialised. It prevails in spiral or hemicyclic types. In others the development may be unequal on different radii, so as to give the flower a lop-sided form; but almost always so that it can be divided by at least one plane of symmetry into two equivalent halves. Such flowers are called *dorsiventral*, *or zygomorphic*, and the Aconite, Laburnum, and Toadflax are examples (Fig. 189). The plane of symmetry is usually the median plane; but sometimes it is oblique, as in the Horse Chestnut; or transverse, as in *Corydalis*. Zygomorphy is very common, it occurs in most families, and it is characteristic of some throughout, as in the Orchidaceae, or Labiatae. Its importance lies in relation to the transfer of pollen by animal agency. The most

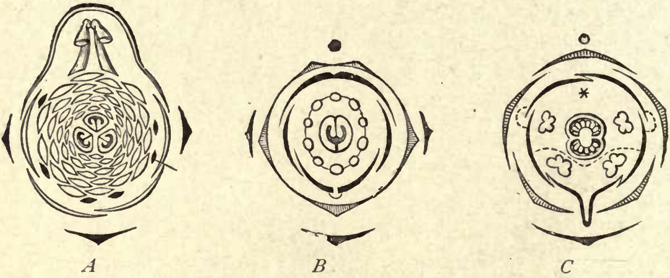


FIG. 189.

Diagrams of zygomorphic flowers. *A*, of Aconite (Ranunculaceae). *B*, of the Laburnum (Leguminosae). *C*, of Toadflax (Scrophulariaceae). (After Eichler.)

perfect mechanisms for this end are found in zygomorphic flowers. It is a derivative or specialised state, and comparison shows that it has been acquired by modification from the radial state, along many distinct lines of descent.

Under these seven headings the most important factors are included which lead to that diversity of floral structure which is so fully illustrated in the Angiosperms. Examples are described in detail in Appendix A, to which reference should be made. Each individual flower may, in point of final analysis, be regarded as a simple shoot bearing sporangia. Structurally its shoot-nature is evident in the less specialised types, though in the more specialised it may be so hidden by peculiarities of form as to be recognisable only after careful analysis and comparison. The several factors are effective in the most varied combinations, so that the analysis which is required to reduce a complicated structure to terms of construction like that of the leafy shoot may demand both skill and insight. The most obvious end served by the mechanisms that result is *the transfer of pollen from the stamen to the carpel*. This is a necessary step in normal reproduction.

For carrying this out, Seed-Plants are dependent upon external agencies, such as water, wind, or animal activity. Moreover, as the Plant is fixed in the soil and immobile, such agencies must be resorted to if the advantage of intercrossing is to be secured. It is such considerations as these which make intelligible the variety and intricacy of the forms which Flowers show.

The fact that the flower is constructed fundamentally on the same plan as the foliage shoot did not escape the attention of the early botanists. Moreover, they noted that it is universally preceded by some form of vegetative shoot in the individual life of the higher plants. In annual plants this is obvious enough : it is only after the establishment of the leafy plant that the flower-buds make their appearance. But in the case of many of the plants that expand their flowers in the early spring the matter is not so simple, and one is apt to forget the swollen underground parts from whose stores the flowers draw their material. It is needless to elaborate by examples the simple fact that in all cases nutrition must precede propagation. It was this fact that formed the foundation of *Goethe's theory of Metamorphosis.* He recognised under this name the process by which one and the same organ, for instance the leaf, presents itself to us in various modifications, such as the foliage leaf, sepal, petal, or stamen. He distinguished as " progressive metamorphosis " those changes of type of the appendages which proceed from the cotyledons or seed-leaves, through the foliage region and bracts to the flower, and finally to the perfected fruit. On the other hand he designated as " retrogressive metamorphosis " that process by which the succession appears reversed ; as for instance in abnormal or doubled flowers, when a stamen or a carpel develops as a petal, or even as a foliage leaf. These general ideas of the relation of the vegetative and floral regions were amplified and made more definite by later writers, and were for a long time widely held. *Thus it became a general belief that the flower had resulted from changes wrought in some pre-existent vegetative shoot.*

So long as we direct our attention solely to the Flowering Plants this opinion might stand. But as the nineteenth century drew on, knowledge of the lower forms greatly increased, especially in the case of such plants as the Ferns and Club-Mosses. This has supplied the material necessary for a revised theory of the origin of the flower. Checked by these comparisons we may now figure, on a basis of fact rather than of semi-poetical surmise, how the flower as distinct from the vegetative region originated in the higher plants. The main point to bear in mind is that the propagative function must have recurred in each fully completed life-cycle throughout descent. Hence the production of sporangia was never an innovation, and they cannot at any time in the course of descent have been imposed upon a pre-existent vegetative system, as Goethe's theory would assume. The facts suggest that *the whole shoot of relatively primitive Vascular Plants was non-specialised. It served general purposes, both for vegetation and propagation. But in the course of evolution of higher types differentiation took place, so that a certain region became exclusively vegetative, while another produced sporangia. Thus a theory of* SEGREGATION *takes the place of a theory of* METAMORPHOSIS. The vegetative phase naturally comes first in the individual life, so as to supply the necessary materials for propagation. Once these two pristine functions were allocated to distinct regions of the plant, each was open to its own distinct specialisation. And so it comes about that while in simple cases there may be some similarity between the flower and the foliage shoot, the two may diverge widely in more advanced types. But however greatly they may differ, the flower and the foliage shoot are to be held as the results of segregation of parts of an originally general-purposes shoot. This gives a natural meaning to those structural resemblances, which are sometimes so striking, between the foliage shoot and the flower which it ultimately bears.

In such discussions as this the antithesis between the flower and the foliage shoot is apt to be drawn more strongly than the facts warrant. The flower is not always clearly defined from the vegetative region. Comparison of the flowers of Cactaceae and Magnoliaceae, and of some Grasses such as *Streptochaete*, show that bracts may merge gradually into floral organs. A further comparison with Conifers, Cycads, and Club-Mosses will confirm the view that the two regions have not always been as distinct as they now appear to be in the Higher Flowering Plants.

The more important lines have now been sketched along which the analysis of floral construction may be undertaken. Such analysis is a necessary basis for comparison, and ultimately for classification. But it will not be pursued further at present. It is also necessary as a step towards realising how the mechanism of the flower works. An engineer cannot properly understand his engine till he has taken it down. But the engine will not work till the parts are again assembled. Similarly the student must not be content with the mere analysis of the flower. After analysis he must assemble the mechanism again, and study it as a whole. *Each flower functionates as a whole*, just as much as any machine. Each part has its proper function leading towards the common end. *That end is the production of the germ contained in the seed. The transfer of the pollen is only one step towards that end, and a comparatively early one.* It is carried out in relation to the showy parts unfolded at the time of blooming, and thus gains an undue prominence. But the interest does not stop when the flower fades. *Fertilisation, which follows after blooming, is actually the central feature, for it initiates the germ.* It is a necessary prelude to the nursing of the germ within the ovule. The protection of the ovule meanwhile within the carpel, itself either free or sunk into the tissue of the axis, is also important as contributing to the final result. Not only then should the flower itself be studied as a whole, but the propagative process also ; and Pollination, with its accessories of form, colour and scent, should be put into its proper place as one incident only, though an essential one, in the complete propagative story.

Note.—Special attention is drawn to the detailed description of various types of floral structure given in Appendix A. The facts there described will illustrate the preceding chapter. They are placed in the Appendix not because they are unimportant, but so that the description of the reproductive process should not be broken by a mass of detailed facts, however apposite those facts may be to the process itself.

CHAPTER XIV.

THE STAMEN AND POLLEN-SAC.

All the facts brought forward in the preceding chapter may be observed under a hand lens, or under low powers of the microscope. But observation under higher powers is necessary for obtaining an intelligible grasp of the details of propagation in Seed-Plants. The minute structure of the outer envelopes can be dismissed briefly. The *sepals*, which are usually green and relatively firm in texture, repeat in their structure, though on a reduced scale, the features of foliage leaves. Their epidermis bears stomata, and the mesophyll below, though small in quantity, contains chlorophyll, and is traversed

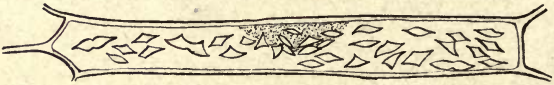


Fig. 190.
Single cell of a petal of *Senecio*, showing numerous chromoplasts of semi-crystalline form. (× 800.) (After Schimper.)

by vascular strands after the manner of other leaves. The *petals* also, though wider in expanse and more delicate in structure, are constructed on a similar plan. But the green of chlorophyll is replaced in them by other colours. The blues and pinks are chiefly due to *colouring matters dissolved in the watery cell-sap* of the cells. But the red and yellow colours are given by bodies called *Chromoplasts*. These are often of irregular crystalline form. They are derived from the plastids of the young cell, and multiply like them by fission (Fig. 190). Sometimes both sources of colour may be present in the same petal, and even in the same cell. The streaky colouring of Parrot Tulips arises from the irregular distribution of the chromoplasts in addition to the soluble colouring. The outer floral envelopes take no direct part in propagation. Indirectly they serve that purpose: the sepals by the protection which they give to the inner parts of the young bud; the petals by giving scent, and a wide expanse of coloured surface, by which means the flower is made attractive. Both parts are subject in special cases to modification of form and character in relation to pollination; but these details must be left aside for the present. After the flower is full blown, the petals wither and fall away. The sepals frequently fall away also, as in Crucifers and in the Buttercup. Sometimes they drop even before the flower is full blown, as in the Poppy. In other cases they persist, as in the Rose, Violet, or Pea, though their further use is not obvious.

FIG. 191.
Stamens of Iris: that on the right shows dehiscence. (After Figuier.)

The *stamens* which lie within are essential for propagation. Their function is to produce *pollen-grains* which, after further development, give rise each of them to two *male fertilising cells*, or *gametes*. The form and structure of the stamens may vary in detail in special cases. But in the great majority of flowers they conform to one simple type, consisting of a cylindrical stalk or *filament*, which is continued upwards into the distal *anther* (Fig. 191). This is two-lobed, the lobes being attached laterally along the filament. While young the outer surface of the anther is turgid, and unbroken. When ripe it opens, sometimes by pores, as in *Solanum*, but usually by longitudinal slits, right and left, which gape widely, as in *Iris* or *Caltha*. Thus the *pollen* is shed as *grains*, usually separate and of yellow colour. The ripening of the stamens coincides with the blooming of the flower; but in cases where the stamens are numerous they may open in

A *B*

FIG. 192.
Sections of the anther of *Caltha*. *A*, before dehiscence, showing the four pollen sacs still closed. *B*, after dehiscence, showing the sacs open, and the slits gaping widely. (Enlarged.) F. O. B.

succession, so that the shedding of the pollen may be spread over a lengthened period. After the pollen is shed the stamens usually fall away, or sometimes they persist in a withered state; but they serve no further function.

If the anther of any ordinary stamen be cut transversely it is found to contain *four loculi*, or *pollen-sacs*, two being placed on either side of a central connective, which is simply a continuation upwards of the filament. A single vascular strand which traverses the filament is continued upwards into the anther, where it fades out usually without any branching (Fig. 192, *A*). However unlike a foliage leaf the stamen so constructed may appear to be, there is no reasonable doubt of its foliar nature. It arises from the axis like a leaf, and in acropetal succession, while in "doubled" flowers it may not unfrequently be seen to be transformed into a petal, or even into a green

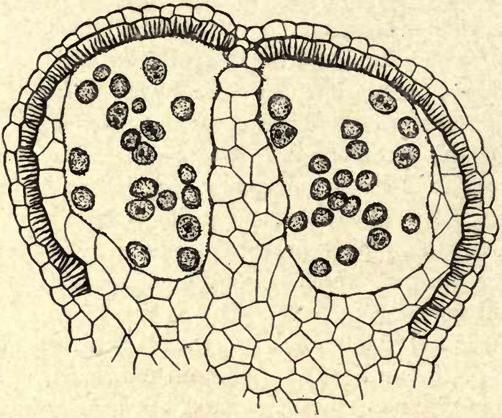


FIG. 193.
Lobe of anther of *Caltha* cut transversely, showing two pollen-sacs at maturity, with the fibrous layer immediately below the epidermis. For details see text. (× 100.) F. O. B.

leaf of the foliage type. But better evidence is obtained by comparison of earlier fossil Seed-Plants, in which the organs bearing pollen-sacs are actually leaf-like.

It may then be accepted that the *stamens are leaves, specialised for bearing pollen-sacs or micro-sporangia.* Each pollen-sac is enclosed till it is ripe by a wall consisting of several layers of cells. In most stamens the slit of dehiscence runs longitudinally, following the line where the walls of the two sacs of one anther-lobe join with the septum that separates them (Fig. 193). There the cell-walls are thin, and the cells themselves are rounded off by intercellular spaces, so that they easily come apart. The slit thus formed gapes widely, owing to the action of the walls of the pollen-sacs. Below their superficial epidermis lies a *layer of fibrous cells*, the inner cell-walls of which are thicker than the outer, while fibrous bars running outwards along their lateral walls prevent radial collapse. The effect on these cells of drying as the anther ripens is that their thin outer walls shrink, while the thick inner wall retains its form. The result of the shrinkage of the outer side of the fibrous layer will naturally be to reduce the curvature of the convex sporangial wall, and the slit gapes widely (Fig. 192, *B*). The dusty pollen-grains are then readily removed. There are various differences in detail of the dehiscence of anthers, particularly in highly specialised flowers. But in all ordinary flowers where the pollen is dry and powdery, the way in which it is set free is essentially like that described.

The pollen itself varies greatly in different plants, in the form and size of the grain, in the sculpturing of its walls, in colour, and in the

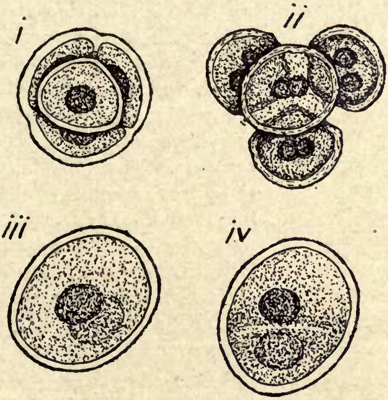


FIG. 194.
Pollen-tetrads and pollen-grains of *Caltha*. (i.) a tetrad, with each cell uninucleate. (ii.) an older tetrad, with the grains almost separated, each containing two nuclei. (iii., iv.) mature pollen-grains, showing the larger vegetative, and the smaller antheridial mother-cell. (× 550.) F. O. B.

dryness or stickiness of its surface. But these differences are only external. *There is a remarkable uniformity of the internal structure of the pollen-grains of Flowering Plants* (Fig. 194, iii. iv.). They are *two-celled.* One cell is usually the larger, and it is called the *vegetative cell,* because it is from it that the pollen-tube is formed, and it does not take any direct part in the reproductive process. It consists of cytoplasm, and a nucleus. The smaller cell is the *antheridial mother-cell*; it also has cytoplasm and a nucleus, and is marked off from the other by a plasmic film, not by a cell-wall. The two-celled state of the pollen-grain may be attained while it is still in the unopened pollen-sac.

The early stages of segmentation of the stamen may be followed by study of the flowers of *Chrysanthemum* (Fig. 195, i.-iv.). The stamen first appears as a rounded papilla of tissue. It is covered by a layer of cells which divide only by walls perpendicular to the surface, so that the layer maintains its identity. It develops into the *epidermis* (i.). The young stamen soon shows four angular projections, which represent the four pollen-sacs. They project owing to the active growth and division of the hypodermal cells (ii. iii.). In the earliest state the hypoderma also appears as a single layer all round (ii.); but as it grows older certain of its cells enlarge at the angles of the section, and divide by walls parallel to the surface. Outer *parietal* cells are thus cut off from inner cells which are *sporogenous*, and give rise ultimately to the pollen (ii. iii.). The outer cells undergo further division by walls parallel to the first, forming usually three cells each (iv.). Of these the outermost provide, after further growth and division, the *fibrous layer*; while the innermost, which adjoins the sporogenous cells, forms part of the nutritive tissue known as the *tapetum*. The sporogenous cells themselves, which are shaded in Fig. 195, ii.-iv., are easily distinguished not only by their origin, but also by their dense protoplasmic contents. The steps thus described are found to be very constant in the anthers of Flowering Plants. They provide material for comparison with other sporangia. There is some latitude, however, in the number of the divisions, and the figures show this even in the single case of *Chrysanthemum*. Where the stamen is large and its walls thick, as in the Lily, more numerous divisions of the hypodermal cells may provide a sporangial wall thickened by extra layers.

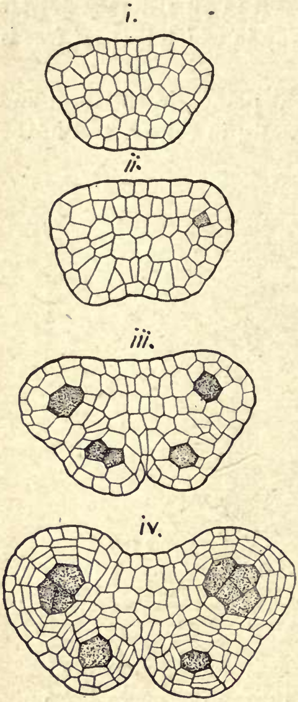


FIG. 195.
Successive stages in the early development of the anther in *Chrysanthemum*. (After Warming.) (× 300.) For details, see text.

As the pollen-sac develops, the layer next below the epidermis first acquires a store of starch (Fig. 197) which is converted later into the thickening of the walls characteristic of the *fibrous layer* (Fig. 193). Within this lie the featureless cells of the intermediate layer. The group of sporogenous cells increases in size, and often also in number of cells by division. Each of these cells is called a *pollen-mother-cell*. The group of them occupies the centre of the projecting sporangium, and is invested by the *continuous sheath of the tapetum* (shaded in Figs. 196, 197). This appears as a single layer of large cells with very thin walls and granular contents. It is the result of development of the cells on all sides adjoining the sporogenous group. Fragmentation of the nucleus frequently happens as its cells grow old. Its function is to nourish the developing pollen. As the grains mature the cells of the tapetum gradually collapse, their substance being absorbed by the pollen. In the mature pollen-sac only vestiges of them remain lining the sac internally (Fig. 193).

The *pollen-mother cells* are all derived by division from the inner product of the hypodermal cells. They vary in number in different anthers. *Caltha* gives an average example, in which from 14 to 16 appear in each transverse section of a pollen-sac (Fig. 196). They are characterised by very thin walls, a dense, non-vacuolated cytoplasm, and a proportionately very large nucleus. At first they are closely fitted together, without intercellular spaces (*a*). But presently the pollen-sac distends, and the pollen-mother cells round themselves off, and become suspended individually in a fluid medium which fills the spaces between them (*b*). Meanwhile the tapetal cells, from which the fluid probably arises, retain their form, though their nuclei often increase by fragmentation.

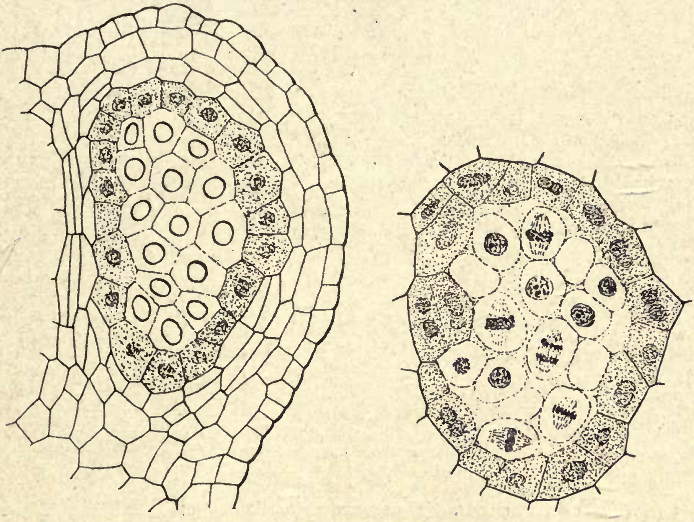


FIG 196.
a, *b*, successive stages of development of the contents of the pollen-sac. See text. (× 100.) F. O. B.

As the pollen-mother-cells separate they enter on the *tetrad-division.* Each nucleus divides first into two, and then into four. These rapidly repeated divisions are characteristic of all spore-formations, and have an important relation to the constitution of the nuclei themselves. The four resulting nuclei are first enclosed in the single protoplast. But soon each is separated by a partition-wall, and is surrounded by a quarter share of the cytoplasm. The *pollen-tetrad* is thus constituted. The four cells are still enclosed by the common wall; but later each cell deposits a special wall round itself. The common wall, which was of a mucilaginous character, is then dissolved, with the result that the four cells become dissociated as independent pollen-grains (Fig. 194, i. ii.). Meanwhile the single nucleus of each has divided, giving the two nuclei present in the mature grain (Fig. 194, iii. iv.).

This description of the development seen in *Caltha* applies for the development of the pollen in all ordinary Dicotyledons. In Monocotyledons the process is essentially the same. But the pollen-mother-cell, after the first nuclear division, is itself partitioned by a wall into two cells, in each of which the second nuclear division follows. The final result is thus the same, except that the arrangement of the tetrad is not tetrahedral, as it usually is in Dicotyledons. But the grains lie in pairs, the longer axis of one pair being at right

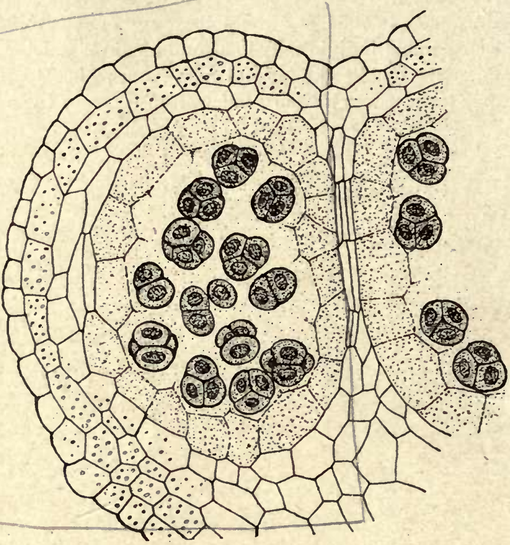


FIG. 197.
A later stage of development of a pollen-sac, showing the young fibrous layer, containing starch. The tapetum (shaded) surrounds the sac in which the tetrads float freely. (× 100.) F. O. B.

angles to that of the other. These are minor points; in all essentials the tetrad-division which produces the pollen is the same throughout Flowering Plants.

For the present this brief description must suffice. But later (Chapter XXXI.) the details of behaviour of the nuclei in this important process of tetrad-division, and chromosome-reduction will be described and discussed at greater length (p. 467). The pollen-grains, as their development shows, are produced from internal tissues of the plant, and are set free by rupture of the superficial tissues. Such bodies are called *spores*, and the pollen-grains being of relatively small size are called *micro-spores*. A step in their production is the *tetrad-division.* The tetrad breaks up later into its *four constituent spores. Tetrad-division is a constant feature in the production of spores in all spore-bearing Plants*, such as Mosses, Ferns, and Seed-Plants. When a marked feature such as this recurs with constancy in a large group of organisms, even though they differ in many other respects, it may be assumed that it has some special significance. In this case the importance of the tetrad-division may in part lie in the provision of numerous easily transferred bodies, which have an essential part to play in the propagative process. But a more important point is that *in the course of the tetrad-division the nuclei undergo the change called REDUCTION.* Certain formed bodies, *chromosomes*, present in constant number in each nucleus on division, are reduced, in the course of the process, to half their original number in each nucleus. All the products of further division of nuclei so reduced have the same smaller number. The ordinary nuclei of the plant have a number of chromosomes which may be represented as "$2x$," and they are called *diploid.* The nuclei that result from reduction are found to have only "x" chromosomes, and are described as *haploid.* The constitution of the nucleus and its behaviour in reduction will be discussed again in detail in a later chapter. Meanwhile we note that *an essential change has occurred in the tetrad-division, and that the nuclei produced within the pollen-grain are themselves haploid.* It is then not simply a separation of vegetative cells that occurs in the production of pollen. The grain as it leaves the anther conveys with it nuclei that differ in an essential feature from those of the ordinary vegetative cells of the Plant. The process of reduction in the tetrad initiates a *sexual phase*, or *Gametophyte.* The result of its further development will be certain cells, which are capable of taking a direct part in sexual reproduction, viz. the *male gametes*, or *sexual cells.*

CHAPTER XV.

THE CARPEL AND OVULE.

THE *Gynoecium*, or *Pistil*, occupies the centre of the Flower. Its office is to produce ovules, and after their fertilisation to nourish and protect them, together with the new germ that each may contain. This nursing function is continued till the time of ripeness, when the Seeds are shed. The Gynoecium is thus the most persistent part of the Flower. While the sepals, petals, and stamens are liable to fall away after the period of blooming, the gynoecium remains attached until the seed is ripe, continuing to draw from the receptacle the nourishment required for the germ. The term *Fruit* is applied to the whole Pistil when fully matured.

The Gynoecium is composed of *Carpels*, which may vary in number in different cases from many downwards to one. Associated with them are the *Ovules*, or *Mega-Sporangia*, which also vary from large numbers in some cases down to one in others. Two parts of the gynoecium may be distinguished by their structure and function. A distal region, which offers at the time of blooming a receptive surface for the pollen-grains: this is called the *stigma*; and a basal part, distended as the *ovary*, which encloses the ovule or ovules. Frequently, and especially in syncarpous pistils, an elongated region intervenes which is called the *style* (Fig. 199).

The Carpels are leaves. Often that can easily be recognised, as in the Pea, where the pod represents a single carpel; or in *Caltha*, where there are many (Fig. 198). In this case they are all separate from one another (*apocarpous*), and their foliar nature is undisguised. Each leaf is folded so as to envelop the ovules borne on its margins, while the midrib is turned outwards from the centre of the flower (Fig. 200). The foliar nature of the carpels is less easily recognised where they are united (*syncarpous*), as they are in the Lily. But even there a transverse section shows by its outline, by the arrangement of the vascular strands, and by the position of the ovules that the compound

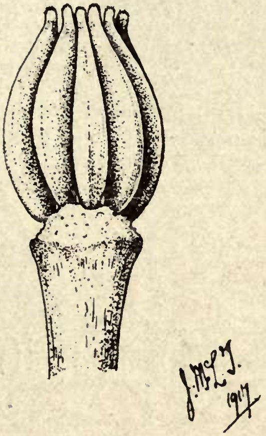


FIG. 198.
Whole gynoecium of *Caltha*, consisting of many carpels, all separate.

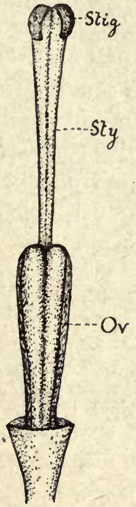


FIG. 199.
Pistil, or gynoecium of Lily, showing the relative positions of ovary, style, and stigma. F. O. B.

structure is referable in origin to three fused leaves (Fig. 201). Moreover cases of partial fusion are found, for instance in *Colchicum*, where the three carpels are fused below, but extend upwards as separate

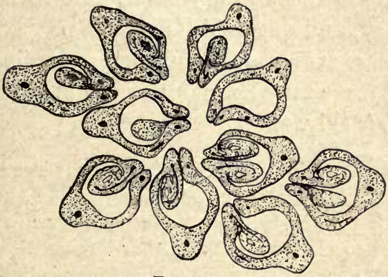


FIG. 200.
Transverse section through the separate carpels, composing the gynoecium of *Caltha*. F. O. B.

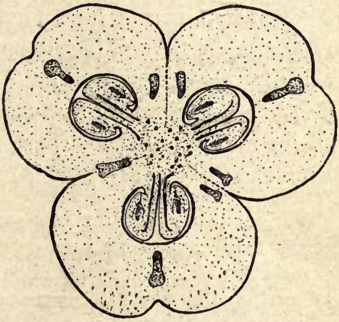


FIG. 201.
Transverse section of the syncarpous ovary of Lily, showing the three folded carpellary leaves, bearing ovules on their margins. F. O. B.

styles. Their relative positions are, however, the same as of those in the completely syncarpous Lily. Biologically the advantage of a coherent gynoecium over that with separate carpels lies in the more effective protection and nutrition of the ovules. But it presents fresh difficulties in the liberation of the seeds when ripe.

The structure of the gynoecium is further complicated by the fact that the carpels are frequently sunk into the tissues of the enlarged receptacle, a condition which serves still more completely the purpose of protection and nutrition of the ovules; for it brings them closer to the nutritive supply that comes from below, and makes a thicker protective wall possible (Fig. 187). Naturally this goes along with fusion of the carpels. The result is a massive body formed partly

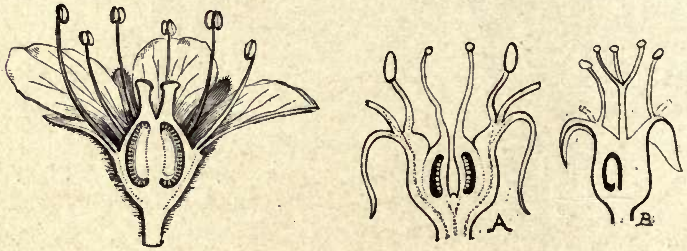


FIG. 202.
To the left, median section of the flower of Saxifrage, showing the carpels half sunk in the receptacle, and coherent for the greater part of their length. (After Figuier.) *A*, similar section of the Quince, showing apparently inferior ovary, but the styles and stigmas separate. *B*, same for Apple, showing styles united, but stigmas still separate. (After Warming.)

from the floral receptacle, partly from the carpels. It is *syncarpous*, and being apparently below the other floral parts it is styled *inferior*. The development of such a gynoecium has been traced in the structurally simple, though highly specialised case of *Chrysanthemum*, where there is only one cavity of the ovary, and one ovule (Fig. 188, p. 239). But in relatively primitive cases there are several loculi, corresponding to the number of the carpels, and there may be many ovules in each, as in the *Quince* (Fig. 202, *A*) or *Iris* (Fig. 203).

Various intermediate states serve to explain how the inferior syncarpous ovary may have come into existence. For instance, in *Saxifraga* the two carpels are united through about half their length, and are partially sunk below the other parts in the tissue of the axis (Fig. 202). Other intermediate states are seen in the Pomeae. For instance, in *Cotoneaster* the flower is little removed from the perigynous state. In *Cydonia* the ovary is more distinctly inferior, but the carpels are not fully united, each having a separate style, while the apex of the abbreviated axis lies in a deep depression between them (Fig. 202, *A*). In the closely related Apple their fusion is more advanced, so that there is a common style, but a distinct stigma for each carpel (Fig. 202, *B*). The last step of fusion would be their coalescence to a single stigma, as is seen in the Lily (Fig. 199). Such fusion of carpels, with or without their sinking into the receptacle, has developed progressively, and has appeared repeatedly in distinct evolutionary lines. The result is the solid and massive gynoecium, whether with superior or inferior ovary. A transverse section of the inferior ovary may still show evidence of its carpellary origin almost as clearly as in the superior ovary. This is seen in *Iris*, where notwithstanding that the carpels are sunk in the receptacle, their structure, and even the arrangement of the chief vascular strands resembles in some degree that seen in the superior ovary of the Lily (Fig. 203). The conclusion follows that in such cases the gynoecium is still to be referred in origin to foliar structure, more or less completely fused with or sunk into the tissue of the receptacle.

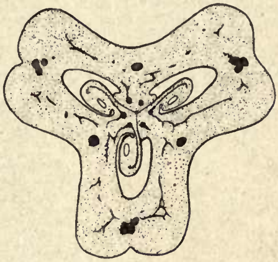


FIG. 203.
Transverse section of the inferior ovary of *Iris*. Compare the superior ovary of Lily, Fig. 201. F. O. B.

The *structure of the carpel*, where it is distinctly leaf-like, as it is in the pod of the Pea, corresponds in essentials to that of a foliage leaf, but simplified. A vascular strand usually traverses each margin, as in *Caltha* (Fig. 200). This is related to the fact that the ovules are seated there; or, as it is described, the *placentation is marginal.* It is probable that this was the regular primitive position for ovules. But sometimes they appear scattered over the inner surface of the carpellary wall, as in the Flowering Rush (*Butomus*), the Poppy, or the Water-Lily. This is described as *superficial placentation*, and it probably originated by the spread of the ovules to the surface. Sometimes they appear as though seated on a prolongation of the axis into the ovarian cavity, as in the Pinks and Primroses (Appendix A). This is called *free-central placentation*, and it also is probably derived from the marginal type, by breaking away the partitions, or septa, of the syncarpous ovary, leaving the margins with their ovules at the centre. Thus the marginal was probably the primitive, as it is certainly the prevalent position for the ovules on the carpellary leaf; and this holds equally for syncarpous ovaries (Figs. 201, 203).

The *Stigma*, or *receptive surface for the pollen-grains*, is at the distal end of the carpel. Where the carpels are separate each has its own stigma, a condition which is probably the primitive state. It is seen in *Caltha* and the Buttercup, the stigmatic area being recognised by its roughened surface. Even where the carpels are united below into a syncarpous ovary, each may separate upwards to form a distinct stigma, as in the Apple or Quince (Fig. 202, *A*, *B*). But in cases which are regarded as more advanced the fusion of the carpels may extend to their tips, and a single stigma is the result, as in the Lily (Fig. 199) or *Datura* (Fig. 204). Even here the receptive surface is lobed, and the number and position of the constituent carpels is indicated by that of the stigmatic lobes. From external observation this is often the readiest guide to the composition of the gynoecium. For instance, the two-lobed stigma of the Compositae accords with the facts of

FIG. 204.
Stigma of Datura with pollen-grains adhering to its surface. (After Figuier.)

development of their flowers, in which two carpels make their appearance (Fig. 188). In *Datura* the two lobes clearly indicate the two carpels of the Solanaceae.

The roughness of the stigmatic surface is due to the outgrowth of the superficial cells as papillae (Fig. 204), the size of which is found to bear a relation to the size of the pollen-grains. The cells are thin-walled, with active protoplasts ; frequently they are moist, or secrete a sticky juice, which helps to detain the pollen-grains in contact with the surface. The grains themselves have sometimes a sticky exterior, which serves the same end. A still more important feature is that the *style, by its elongation carries the stigma upwards to a level suitable for* *the deposit of the pollen* (Fig. 187). In some cases the style is absent, as in the Buttercup or Nettle. It is a feature of variable occurrence, resulting from intercalary growth which is adjustable according to the proportions of the other parts. Extreme cases are seen in the *Crocus* or in *Colchicum*, where the ovary is underground, while the style, which is six inches or more in length, carries the stigma several inches above ground, to a level a little in advance of the stamens. In the Gamopetalous Dicotyledons, and in many Monocotyledons the cylindrical style is proportional in length to the tube of the corolla, as is seen in Tobacco and Gloxinia, or in *Lilium auratum* and *Narcissus*.

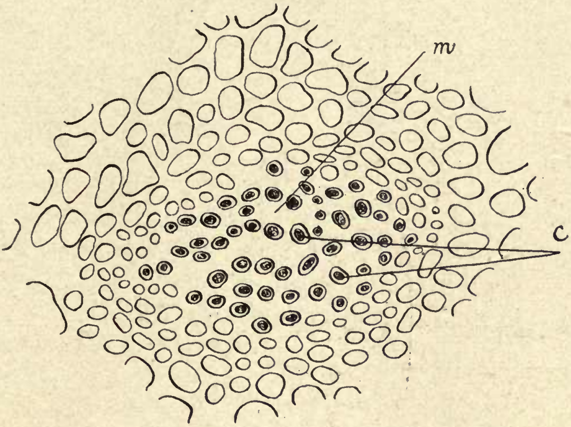


FIG. 205.
Transverse section of the style of *Salvia*, showing the cells of the conducting tissue (*c*) with swollen mucilaginous walls (*m*). (After Capus.)

The style is sometimes traversed by an open channel, so that direct access can be gained to the ovarian cavity from the stigma; this is the case in the Violet and Mignonette. But where the channel is narrow it is commonly filled with a mass of mucilage derived from epithelial cells which clothe its surface. This is seen in the Lily and Rhododendron, in both of which a separate groove from each of the stigmatic lobes leads downwards to the common conducting canal filled with mucilage. In other cases there is no actual canal, but a column of lax tissue with mucilaginous walls traverses the style, and serves as a conducting tissue. This is found in *Salvia* (Fig. 205); also in the Corn Cockle (*Agrostemma*), and in the Mallow. In such cases the conducting tract is connected upwards with the separate stigmas, while downwards the channel branches so as to lead to the several loculi of the ovary.

The *ovule* at the period when it is ready for fertilisation is more or less oval in form, and it is seated upon a stalk, the *funiculus*, which is usually short (Fig. 206). It consists of a central body of conical form, which is called the *nucellus*. This is the actual *mega-sporangium*. It is invested by one, and frequently by two *integuments*, which are attached to its base, and cover it closely, leaving only a very narrow channel

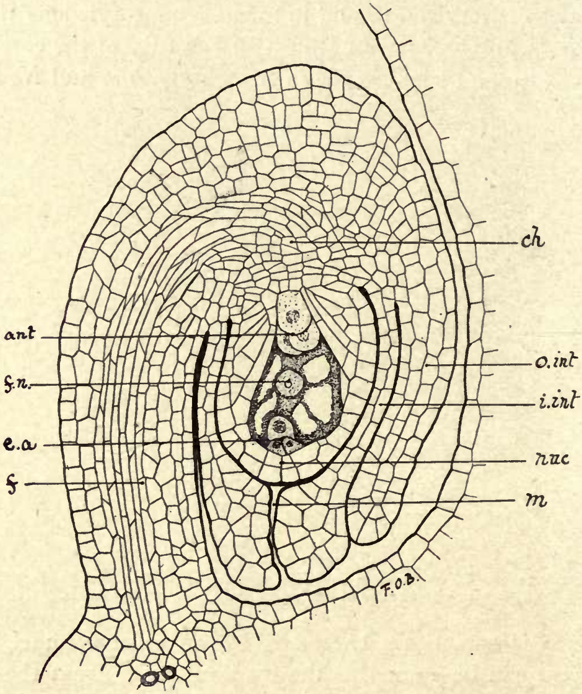


FIG. 206.

Median longitudinal section of an ovule of *Caltha*, at the period of fertilisation. *f*=funiculus. *ch*=chalaza. *o. int*=outer integument. *i. int*=inner integument. *nuc*=nucellus. *m*=micropyle. *e. a*=egg-apparatus. *ant*=antipodals. *fn*=fusion nucleus. (× 110.)

open at the apex, which is called the *micropyle*. The opposite end, where it is attached to the funiculus, is called the *chalaza*. A vascular strand, springing from the vascular system of the carpel, traverses the funiculus, but stops at the chalazal end of the nucellus. This leads up the supplies to the base of the sporangium. The form of the ovule varies. Sometimes it is *straight*, as in the Rhubarb or Dock (Fig. 211); sometimes the body of the ovule is itself *curved*, as in the Kidney bean or Shepherd's Purse. In the great majority of cases the body of the ovule is straight, but it is *inverted* or *anatropous*, so that the micropyle lies close to the attachment of the funiculus on the carpel. This is seen in Fig. 206, which shows an ovule of *Caltha* cut in median section, at the time when it is ready for fertilisation. The nucellus is the essential part of the ovule, the integuments and the funiculus being accessory. They provide respectively for external protection, and attachment with conduction of supplies. Moreover, the nucellus is the part first formed. In a young state it may be

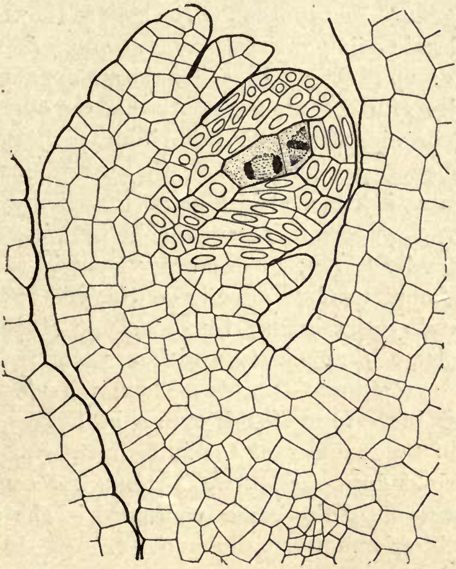


FIG. 207.
Median section of a young ovule of *Caltha*, anatropous curvature still incomplete, and the nucellus only partially covered by the integuments. The spore-mother-cell has divided once, and the second division to form the tetrad is already indicated. (× 200.) F. O. B.

found already well advanced, though the integuments are incomplete, and the funiculus is only beginning to assume that curvature which results in the inversion of the mature ovule (Fig. 207).

At the period of blooming the nucellus consists of a peripheral covering of thin-walled cells, of varying thickness in different groups of plants, enclosing one large cavity, which, though its contents are complex, is developed from a single cell. This is the *Embryo-Sac*, or *Megaspore.* It attains its large size by encroaching on the adjoining cells as it develops, by a process of digestion; this leads to their collapse, and the final absorption of their substance. The sac is limited by a very thin cell-wall, and is lined by dense granular protoplasm. Within it seven nuceli are seen, of which one of large size is about the centre (*fn.*). As these contents of the embryo-sac are almost constant in Flowering Plants, and are all accessory to the production of the new germ, they demand special attention. There are two groups of three cells each, one fixed at the micropylar end, the other at the chalazal end of the embryo-sac. The latter are often large, with well-marked nuclei, each of which is surrounded by an area of granular cytoplasm marked off by a plasmic film, not by a cell-wall. It is called the *antipodal group* (*ant.*), and it occupies the base of the embryo-sac, just above the chalazal ending of the vascular strand. At the micropylar end is another group of three cells, called the *egg-apparatus* (*e.a.*). One of the cells projects further into the cavity than the other two: it is the *Ovum*, or egg-cell which after fertilisation initiates the new germ. The other two are of equal size, but smaller; they are called the *Synergidae*. The egg-apparatus is attached just below the micropyle. In *Caltha* two layers of cells are seen to intervene (Fig. 206), but in other plants the number may be larger; on the other hand in many ovules the embryo-sac is found to abut directly on the micropyle. The large cavity of the embryo-sac is filled by vacuolated cytoplasm, while in the centre a large *fusion-nucleus* with a prominent nucleolus is suspended by cytoplasmic threads. Though ovules of Flowering Plants may vary in the form of their ovules, in the complexity of their construction, in the number of the integuments, and even in the number of their embryo-sacs, there is a marked constancy in the number and position of the bodies contained in the embryo-sac at the time of fertilisation.

The following description of the development of the ovule relates primarily to the type seen in the relatively primitive family of the Ranunculaceae. It appears at first as a rounded papilla of tissue, which develops directly into the nucellus or megasporangium. By active growth and cell-division it is carried up upon the elongating funiculus. Meanwhile by outgrowth of a ring of tissue at the base of the nucellus the inner integument first appears. The outer integument follows as a growth on the side which will be turned outwards as the ovule becomes inverted; later it coalesces with the stalk so as to invest the nucellus on all sides except that of the stalk (Fig. 207). As the ovule grows older the curvature increases till it is completely inverted. Meanwhile the integuments extend over the nucellus, covering it in, except for the narrow channel of the micropyle (Fig. 206).

The chief interest lies in the *origin and development of the embryo-sac.* It has been stated that the nucellus is a megasporangium, and the embryo-sac a megaspore. It is because of the manner of their development that these parts are so recognised. The young nucellus first appears as a hemispherical upgrowth: it consists internally of a number of radial rows of cells, covered by a superficial layer. The latter divides in *Caltha* into two or more layers at the tip of the nucellus, forming a cap of tissue covering the radial rows within. It is from the central row of the internal cells that the embryo-sac arises. The condition in *Caltha* is relatively simple. The terminal cell of the central row undergoes division into two, and then into four (Fig. 207). This is in fact a *tetrad-division*, and the mother-cell which divides is of hypodermal origin. It has been shown that this division is accompanied by *reduction of chromosomes* of the nuclei to the half number, as in the pollen-tetrad. The resulting four cells are arranged in a row; pollen-tetrads are sometimes found to have the same arrangement. The conclusion follows that *the tetrad thus produced in the ovule is the correlative of a single pollen-tetrad, and each of the cells might become a spore.* This actually happens in the pollen-sac; but in the ovule as a rule only one of the four potential spores develops further. *The lowest cell of the four* enlarges at the expense of the others, which collapse, and are crushed out of shape. The embryo-sac encroaches also on the surrounding cells of the nucellus, which give way to allow of its increase in size. Thus, as shown by its development, the *embryo-sac is the single spore of a tetrad*: as it develops to a large size it is styled a *mega-spore*.

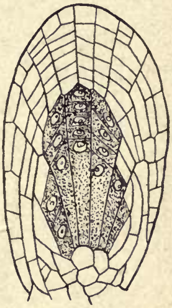


FIG. 208.
Young nucellus of ovule of *Rosa livida*. See text. (After Strasburger.)

In other cases the structure may be *more complex than in Caltha.* A considerable number of Flowering Plants show rapid growth and division of the superficial cells at the tip of the nucellus, so as to form a considerable pad of tissue covering the hypoderma. This is seen in *Rosa livida* (Fig. 208), which also shows numerous hypodermal cells with dense contents, each divided into a cell-row. The basal cell of each row is an embryo-sac mother-cell; the distal cells are parietal cells, comparable with the parietal cells of the pollen-sac (compare Fig. 195). There is thus in *Rosa* a plurality of mother-cells, as is usual in pollen-sacs; while the parietal cells, which are absent in *Caltha*, are here present, and strengthen the comparison with the pollen-sac. Such conditions, which are not infrequent among the more primitive Dicotyledons, indicate that the pollen-sac and the ovule, though differing in form, have essential features in common. Both are sporangia, though they have diverged in details of development.

Other ovules again are *simpler than Caltha.* For instance, in *Monotropa* the nucellus is represented only by a single layer of cells, surrounding one central row, which consists of the embryo-sac itself and two sister cells (Fig. 209, i.). Here there are no parietal cells, and the tetrad itself is represented only by three cells, the uppermost cell of the tetrad not having undergone the second division. The two sister cells are later disorganised, and make way for the embryo-sac; and finally the single layer of the nucellus is also absorbed (Fig. 209, viii.); so that *at fertilisation the embryo-sac is all that represents the nucellus.* A still simpler condition as regards the origin of the embryo-sac though not of the whole structure, is seen in *Lilium*. Here, as in most Monocotyledons, the parietal cells are absent. Further, the hypodermal cell of the central row itself becomes directly the megaspore-mother-cell, and reduction takes place not in the preparation of the mother-cell, but during the first divisions within it. The whole development is here condensed, and stages seen elsewhere are entirely omitted.

There is thus considerable latitude in the details of the nucellus, associated with marked differences in its bulk. Speaking generally, the nucellus is more bulky in relatively primitive types, such as the Rosaceae and Ranunculaceae, and especially in the Fagales. It is less bulky in advanced types, such as the Gamopetalous Dicotyledons, or the Orchids. But they often make up for this by the elaborate structure of their single integument.

In sharp contrast to this variability of the nucellus, or megasporangium in Flowering Plants, is the dead level of uniformity shown by the embryo-sac or megaspore, and its contents. So great is this that,

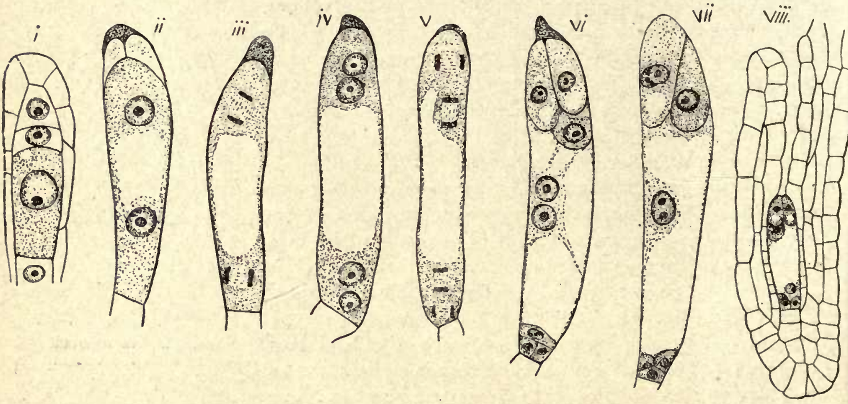


FIG. 209.
Stages in the development of the embryo-sac of *Monotropa*, after Strasburger. See Text below. (i.-vii. × 400. viii. is less highly magnified.)

putting aside the few exceptions that exist, one description will serve for all Angiospermic Plants. It is based upon the observations of Strasburger on the transparent ovules of *Monotropa* (Fig. 209). The lowest of the three cells resulting from division of the megaspore-mother-cell is the future embryo-sac (i). It enlarges at the expense of the other two, which collapse, and their disorganised remains appear as a cap covering the micropylar end of the sac (ii.-vi.). The nucleus divides into two, which pass to opposite ends of the sac, while a vacuole appears between them (ii.). They again divide (iii.), with the result that two nuclei are formed at either end (iv.). These again divide (v.), and the resulting nuclei arrange themselves in the characteristic way common to embryo-sacs (vi.). Three are grouped at either end, each surrounded by its own area of cytoplasm, limited by a plasma-film. Those at the chalazal end form the *antipodal* *group*; those at the micropylar end form the *egg-apparatus*. The latter consists of the *two synergidae* which occupy the extreme apex, and the *ovum* attached rather lower. The odd nuclei from either end approach one another, and finally coalesce (vii.) to form the *central fusion-nucleus*. The embryo-sac is then ready for fertilisation.

All the nuclei resulting from this development of the contents of the embryo-sac are *haploid*. Reduction has already taken place in the divisions of the mother-cell. The embryo-sac, or megaspore, being one of the products of that division, its nucleus is already reduced. The whole group of nuclei, together with the cytoplasm that surrounds them, may be recognised as the *sexual phase* or *gametophyte*. It is characterised by differing in the constitution of its nuclei from the ordinary vegetative cells of the plant. The ovum is that cell of the gametophyte which will be fertilised. It is the *female gamete*, or *sexual cell, which is to take part in sexual reproduction*.

CHAPTER XVI.

POLLINATION AND FERTILISATION.

"POLLINATION" and "Fertilisation" are often used as synonymous terms. This may have been natural when in 1793 Sprengel published his novel observations under the title "The Secret of Nature discovered in the Structure and Fertilisation of Flowers." But at the present day there is little excuse for such laxity. It is well to be clear in the correct meaning of these words when applied to the Higher Flowering Plants. By "pollination" is meant merely the transfer of the pollen from the anther to the receptive surface of the stigma. By "fertilisation" is meant the actual coalescence of two cells: the one is the male gamete derived from the development of the pollen-grain; the other is the ovum contained within the ovule. Obviously some interval must elapse between the events of pollination and fertilisation; it is usually short, but may in extreme cases be as long as a year, or more. *Pollination precedes fertilisation in the Flowering Plant, and is a means to that end; but fertilisation is the end itself.*

The mechanical problem of propagation in Flowering Plants is complicated by the fact that the Plants themselves are immobile. Being rooted in the ground they cannot like the Higher Animals move to seek their mate. The cells that are to carry out fertilisation, viz. the male and female *gametes*, are produced more or less widely apart from one another. They are themselves incapable of movement, while one of them (the ovum) is deeply embedded in the tissues of the ovule, and covered in by the carpel also. This brings the advantage of protection and nutrition of the germ, but it also greatly complicates the problem of sexual propagation. The steps that are necessary to carry it out are first the transfer of the moveable, though non-motile pollen-grain from the anther to the surface of the stigma of a corresponding plant. That transfer is called *Pollination.* The second step is the *germination of the pollen-grain*, with the formation of a *pollen-tube*, which makes its way from the stigma to the micropyle of the ovule, and conveys the contents of the pollen-grain or microspore to the embryo-sac, or megaspore. The final step is the fusion of the *male gamete*, which the tube conveys, with the *female gamete or ovum*. This fusion is called *Fertilisation*. These several events must be considered separately and in their natural succession.

The distance through which the pollen-grain must travel from the pollen-sac to the stigma varies greatly. In flowers such as the Buttercup, containing both stamens and carpels (*hermaphrodite*), the distance may be small. But in many cases only stamens or carpels are produced in the individual flower, and the grains must then be transferred from one to the other. If the staminate and pistillate flowers are borne on the same plant, the condition is described as *diclinous*, as in the Hazel, Beech, or Oak. They may, however, be borne on distinct plants, which are then styled *dioecious*, as in the Rose, Campion, or Willow. These are examples of the separation of the pollen-sacs and ovules *in space*. But there may also be separation of them *in point of time*. For even where they are seated side by side the pollen-sacs may not shed their pollen at the time when the stigma is ready to receive it. Two possible cases exist. The stamens may shed their pollen before the stigma of the same flower is fully matured, as in the Willow-herb, or in the Compositae. This is the more common state, and it is described as *protandrous*. Or the stigma may mature first, and be no longer receptive when the stamens of the same flower shed their pollen. This is the less common state, and it is seen in the Figwort and Plantain. It is described as *protogynous*. Obviously the practical effect is the same as the separation in space, for in either event the pollen must be brought from elsewhere, if fertilisation is to succeed. In such cases the distance to be traversed may be considerable, and the plant has no means of its own for making the transfer.

Use is then made of outside agencies, such as the movements of wind or water: or the mobility of animals is taken advantage of. The mechanism of flowers has been specialised in the most remarkable manner in accordance with these methods of transfer. Where use is made of *wind* the flowers produce abundance of dry dusty pollen, easily shaken out in clouds from anthers often balanced on very flexible filaments. The stigmas meanwhile are much branched and feathery, so as to expose a large surface for catching the grains. These features go with close grouping of the flowers, which are individually small and inconspicuous. Where *animal agency* is used, the flowers are attractive and conspicuous by their scent, by honey-secretion, and by widely expanded floral envelopes of bright colour. The latter attract the eye, the former the other senses of the animal, and lead him to visit the flower for his own purposes of gathering honey or pollen. Incidentally the floral mechanism is so arranged, in size and form of the parts, that pollen, often of a sticky nature, is deposited on his body as he visits the flower. The flower may be so formed as to lead him, for sake of convenience, to take a definite position: consequently the pollen is deposited on a definite part of his body (Fig. 210). The result of repeated visits to a succession of flowers of like construction will then be that, if the stigmas correspond in position

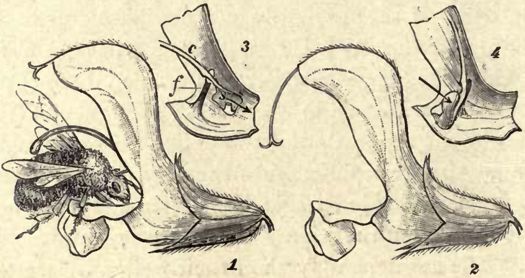


FIG. 210.

Pollination of *Salvia pratensis*. 1, Flower visited by Humble Bee, showing the projection of the curved connective from the helmet-shaped upper lip, and the deposit of the pollen on the back of the Bee. 2, Older flower, with connective withdrawn and elongated style. 4, the staminal apparatus at rest, with connective enclosed within the upper lip. 3, the same when disturbed by the entrance of the proboscis of the Bee in the direction of the arrow. *f*=filament. *c*=connective. *s*=the obstructing half of the anther, which produces no pollen. (After Strasburger.)

to the spots on which he bears the pollen, they may probably receive some part of it. Thus unwittingly he will have been the agent of transfer of the pollen from the pollen-sac to the receptive stigma.

Such mechanisms have been elaborated in the course of Descent in an infinite variety of detail. This is the biological meaning of the attractive features which flowers have assumed. It may even be seen how certain floral types have been adjusted in relation to the visits of certain animals, and show development parallel with them. A good instance is that of the Aconite and the Humble Bee, to whose visits the Aconite flower offers convenient access. A study of their distribution across Europe and Asia shows that the northern limit of occurrence of the two organisms almost exactly coincides. This suggests the importance of the Humble Bee in the transfer of the pollen of the Aconite, while the food which the flower offers may in some measure react in determining the distribution of the bee. The methods of transfer of the pollen may thus be varied. But the essential feature of them all is the same, viz. the conveyance of an immobile body essential for propagation from the pollen-sac, where it is produced, to the surface of the stigma where it can germinate. (For further details on pollination see Appendix A.)

The *germination of the pollen-grain* takes place normally on the stigma. (Figs. 211, 212.) But it can be induced in a nutritive medium, apart from the stigma, such as a solution of cane sugar of suitable strength. This makes it possible to observe the origin and behaviour of the pollen-tube. The germination may be very rapid. From fresh pollen of the Wild Hyacinth, placed in a 7-10 p.c. solution, pollen-tubes will be produced at a normal summer temperature in about 15 minutes, and in an hour will have grown to a length several times the diameter of the grain. In some cases the structure of the wall of the grain does not indicate where the tube will be formed. But in others its origin is determined structurally. In the Willow-herbs and Geraniums three points of origin are present on each grain. Frequently their number is greater, as in the Corn Cockle (Fig. 212, *A*); but of the 40 or 50 points of exit there seen, only one gives rise to a tube. A curious exception is seen in the Mallow, where numerous tubes emerge, which firmly anchor the grain. (Fig. 212, *B*.)

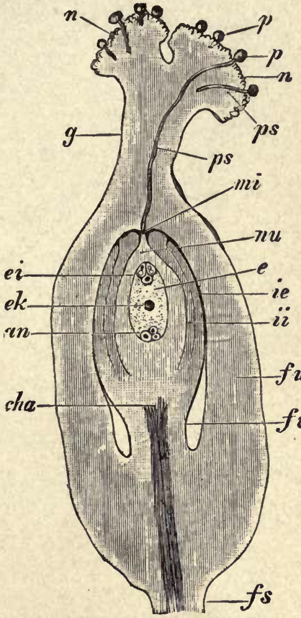


FIG. 211.
Ovary of *Polygonum Convolvulus* at time of fertilisation. *fs*=base of ovary. *fw*=wall of ovary. *fi*=funiculus. *cha*=chalaza. *nu*=nucellus. *mi*=micropyle. *ii*=inner integument. *ie*=outer integument. *e*=embryo-sac. *ek*=central fusion nucleus. *ei*=egg-apparatus. *an*=antipodal cells. *g*=style. *n*=stigma. *p*=pollen-grains. *ps*=pollen tubes. (×48. (After Strasburger.)

The effect of external influences upon the growth of the tube can be studied in the cultures. If grains be germinated in a suitable solution under a cover-glass, the tubes, as they first issue, point indiscriminately in all directions. But soon those near the margin turn inwards from the source of free Oxygen: they are *negatively aerotropic* (Fig. 213, *A*). If a similar culture be prepared, and a piece of the style and stigma of the same species be introduced with the pollen-grains, the tubes curve towards it, and especially towards the cut surface (Fig. 213, *B*). They are *positively chemotropic*. Their behaviour on the stigma, where they take a course in close contact

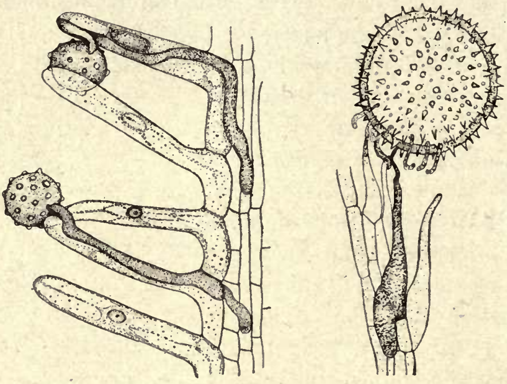


FIG. 212.

A = Pollen-grains of Corn Cockle (*Agrostemma*) showing numerous possible points of origin for pollen-tubes, but only one tube, which penetrates at once a papillar cell of the stigma. *B* = a similar condition in Mallow (*Malva*), but here numerous small tubes are formed for attachment. (After Strasburger.) (× 120.)

with the moist cell-walls, shows that they are also *positively hydrotropic* (p. 128). These three factors are effective in deciding the

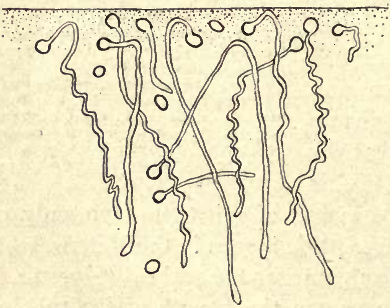


FIG. 213, *A*.

Pollen grains germinated in a nutritive medium, under a cover glass, of which the margin is shown. The tubes curve away from the margin, that is, away from the supply of oxygen. (After Molisch.)

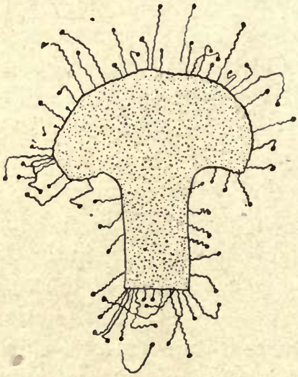


FIG. 213, *B*.

Result of culture of pollen-tubes of *Narcissus Tazetta* in neighbourhood of the style and stigma, in 7 per cent. sugar after 16 hours. Diagrammatic. (After Molisch.) (× 10.)

course of the tube when it germinates normally upon the stigma. They lead it to apply itself closely to the surface cells.

On germination the contents of the pollen-grain pass over into the growing tube. The nucleus of the vegetative cell with its cytoplasm usually passes out first, while the *antheridial-mother-cell* is embedded in the rearward part of the vegetative cytoplasm. It soon *divides to form two gametes*, the nuclei of which follow the vegetative nucleus (Fig. 213, *A*). As the tube lengthens, the grain as well as the older part of the tube is thus emptied of its contents. Successive lengths are then shut off from the distal part of the tube that is still full, by plugs of cellulose, so that as the tube advances it is still possible to preserve its turgor. Thus provided, the tube can advance through long distances to reach the ovule. (Compare Fig. 211.)

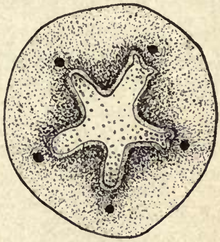
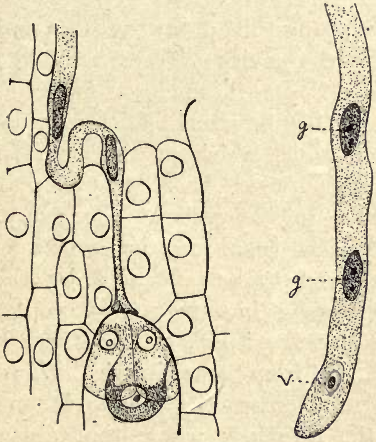


FIG. 214.
Transverse section of the style of *Rhododendron*, showing the five-rayed channel lined with epithelium, and filled with mucilage: it is traversed by the pollen-tubes, which appear as compressed dots in the section.

Germinating on the surface of the stigma the negative aerotropism, positive hydrotropism, and positive chemotropism all lead the tube to a close relation with its moist tissues. Where there is an open channel the pollen-tube does not need to penetrate the tissue. Even where, as in Lily or Rhododendron, the channel is filled with mucilage the tubes penetrate the secretion, but not the cells which produce it (Fig. 214). There is little apparent difference in those cases where, as in *Salvia*, there is conducting tissue with mucilaginous walls (Fig. 205); for there the pollen-tubes penetrate the mucilaginous middle lamella, passing between the cells themselves. This is in fact the commonest way for the tube to enter the tissue of the stigma, and it is well illustrated in the Grasses. Here the tubes force their way between the stigmatic cells, penetrating their middle lamella.



B FIG. 214 *bis*. *A*

A, Pollen-tube of *Orchis latifolia* teased out from the ovary. *v*=vegetative nucleus. *g*, *g*=gametes. (×500.) *B*, pollen-tube of the same penetrating the micropyle: its gametes still in the tube. The two synergids and the ovum (shaded) are clearly shown. (×300.) (After Strasburger.)

But occasionally the cells of the stigma are themselves perforated. This is seen in the Corn Cockle (*Agrostemma*), where the pollen-tube traverses the delicate cell-wall of the stigmatic papilla (Fig. 212, *A*).

The protoplast of the perforated cell is not killed, and it may even continue its movements for a time, and retain its turgescence. The tube passes out between the walls of the subjacent conducting cells, and continues its course in that way. The Mallow behaves similarly, with the further feature that a number of tubes are formed from each of the large grains; but only one develops of large size, the rest serve to fix the grain on the surface of the stigma, the large tube conveying the essential contents (Fig. 212, *B*). It thus appears that pollen-tubes behave upon the surface of the stigma like the filaments of parasitic Fungi, which similarly either follow the surface of the invaded tissue or grow between its cells; but sometimes they penetrate the cells themselves. There is no doubt that in its course the pollen-tube also draws nourishment from the tissue it traverses.

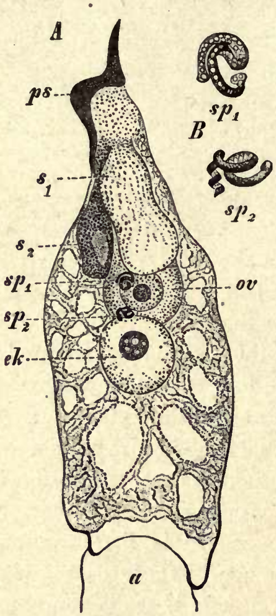


FIG. 214 *tris*.

A, embryo-sac of *Helianthus annuus* (after Nawaschin). *B*, the male nuclei more highly magnified. *ps*=pollen-tube. $s_1 s_2$=synergidae. sp_1, sp_2=mal enuclei. *ov*=egg-cell. *ek*=central fusion-nucleus of embryo-sac. *a*=antipodal cells. sp_1 fertilises the egg; sp_2 fuses with the fusion-nucleus of the embryo-sac. (From Strasburger.)

Passing thus down the style and into the cavity of the ovary, the tube is often conducted mechanically by directing hairs towards the ovule, which in the common inverted type has its micropyle close to the wall of the ovary. The last part of the course is believed to be influenced by the synergids; in some cases a drop of fluid, derived perhaps from them, is exuded from the micropyle. Whatever the influences may be, the tube enters the micropyle and impinges closely on the apex of the nucellus; where that tissue has already been absorbed, it may advance directly upon the embryo-sac, close to the egg-apparatus (Fig. 213, *B*).

The passage of the pollen-tube direct to the micropyle is the usual, and probably the primitive course. Fertilisation in that way is called porogamy. But in a considerable number of plants it takes a course through the superficial tissues of the ovule. Sometimes it passes through the funiculus to the chalazal end of the embryo-sac, as in the Walnut and *Casuarina*; this is called chalazogamy. Sometimes an irregular course may be pursued, by traversing the integuments, as in the Elm. But here the course appears to be very inconstant. It is doubtful whether these irregularities have any special significance, but it is worthy of remark that they occur in relatively primitive Families of Flowering Plants.

The pollen-tube on entering the micropyle conveys with it the two male gametes enclosed in the cytoplasm of the tube (Fig. 213, *A*). Probably the turgor of the contents has its effect in rupturing the soft tip of the tube, and extruding its contents. The nuclei of the two gametes can shortly afterwards be recognised in the embryo-sac. The one passes into the ovum and fuses with its nucleus. The result of fusion of the male and female gametes is the *zygote*. The other passes on to the central fusion-nucleus and coalesces with it (Fig. 214). The mechanism of the movements within the embryo-sac is uncertain. It has been suggested that protoplasmic streaming may assist it. On the other hand, the peculiar form which the male nuclei sometimes take suggests independent movements, like those of the sperms of lower plants to which they correspond functionally. Meantime the synergids shrivel, and begin to disorganise. Clearly their function is completed on fertilisation.

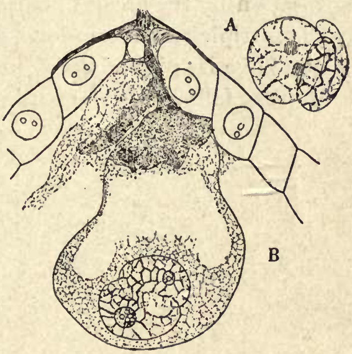


FIG. 215.
Behaviour of the male and female nuclei of Lily in fertilisation. (Mottier.) *A*, vermiform male nucleus applied to the egg-nucleus (*Lilium Martagon*). *B*, egg-cell of *Lilium candidum* showing sexual nuclei in act of fusing. The nuclear membranes have disappeared at the place of contact.

In the case of *Lilium* the more or less spiral form of the male nucleus, when it penetrates the ovum, has been seen to be retained till it is applied to the nucleus of the ovum. But the nuclei gradually become alike in shape, size, and structure. Both are in the resting condition, and have a nucleolus (Fig. 215). The nuclear membrane then disappears at the place of contact, their cavities become one, the chromatin-reticulum of the one unites with that of the other, and the resulting fusion-nucleus can scarcely be distinguished from the nucleus of an unfertilised egg. Finally the nucleoli fuse also. The details of the fusion of the second male nucleus with the central fusion-nucleus of the embryo-sac in *Lilium* resemble those in the egg, but the process is complicated by the fact that it may synchronise with the fusion of the two polar nuclei, so that a triple fusion may be seen actually in progress (Fig. 216). But in most plants the polar nuclei fuse before the access of the second male gamete.

The act of Fertilisation in the Higher Flowering Plants is then a double one, involving the ovum and the central fusion-nucleus on the one hand, and the two male gametes on the other. The nuclei of the male gamete and ovum are both haploid, being cells of the gametophyte generation, derived from spore-mother-cells which have undergone reduction. The fusion of the gametes restores the original number of chromosomes. *The nucleus of the zygote is diploid, and that diploid cell originates the new germ.* The central fusion-nucleus had already resulted from the fusion of the two polar nuclei. On its fertilisation by the second male gamete a third nucleus coalesces with it. This triple fusion is unique, so far as present observation extends. It may have its physiological importance in relation to the developments that follow, for the triple fusion initiates the endosperm.

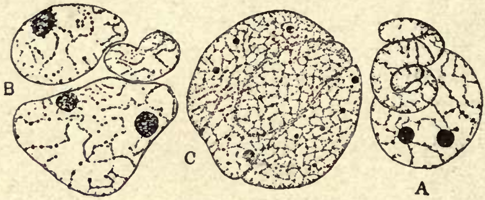


FIG. 216.

Fusion of the second male nucleus with the polar nuclei in *Lilium Martagon*. *A*, an S-shaped male nucleus applied to the upper polar nucleus. *B*, the second male nucleus (shown only in part) and the two polar nuclei close together. *C*, all three nuclei fusing. (After Mottier.)

An important feature characterising the intricate changes in the embryo-sac of Flowering Plants is the extraordinary constancy in the number and behaviour of the cells involved. Plants which differ widely in form, internal structure and biological character, as well as in the number and relation of their floral organs show a remarkable uniformity in these details. Exceptions do exist, but they are few relatively to the majority which conform. This indicates that probably each step is significant in the success of the sexual propagation, though it is not possible to assign with certainty its exact function to each. One general conclusion follows from comparison with forms lower in the scale, though the foundations for it can only be given on a later page; it is that the parts directly involved in the sexual propagation of Flowering Plants represent, in a vestigial form, parts which are more fully represented in more primitive organisms. They all belong to the Gametophyte, or Haploid Generation. Here they appear as only a few cells contained on the one hand in the microspore, or pollen-grain, and its tube; on the other in the megaspore, or embryo-sac. But these represent in their position in the life-cycle that haploid generation which will be seen later in larger proportions and greater independence in such plants as the Ferns and Mosses. In either case, however, it is *Syngamy*, that is the fusion of gametes to form a zygote, which *closes the haploid phase*. This event forms the starting point for the new diploid individual, which is the *Germ* or *Embryo*.

CHAPTER XVII.

THE EMBRYO AND THE SEED.

In normal cases if no pollen-tube arrives at the micropyle of the ovule, and the ovum is consequently not fertilised, the ovule develops no further. But if fertilisation by a pollen-tube has been carried out, changes follow not only in the ovum itself and the other contents of the embryo-sac, but also in other parts of the ovule. The term *Seed* is applied to the body which results from this further development of the ovule, while the germ which originates from the fertilised ovum is called the *Embryo*.

After fertilisation the earliest changes appear in the embryo-sac itself. The Synergidae shrivel, and a cell-wall is deposited round the *fertilised ovum*, or *Zygote*, which remains attached at the micropylar end of the embryo-sac. It soon elongates, its free end extending into the cavity of the sac. Meanwhile its nucleus, which has resulted from the fusion of the male and female nuclei, divides, showing the double number of chromosomes characteristic of the *diploid* generation. The zygote then divides into two cells by a transverse wall, and this may be followed by further divisions in planes parallel to the first; so that a simple filament, or *Pro-embryo*, is formed (Fig. 217, i.). The very first division of the zygote stamps the polarity of the pro-embryo, and from that point on defines its apex and base. The basal end of the pro-embryo remains attached to the micropylar end of the sac, the apical end projects into the cavity, and produces the embryo. It is a significant fact that in the great majority of Flowering Plants, though not in all, this filamentous stage, showing polarity and consisting of a varying number of cells, appears first. It has the practical result of carrying the embryo deep down into the sac, but it may also have a phyletic meaning, as indicating an ancestral filamentous construction. The pro-embryo then differentiates into two regions: a free apical part which develops into the massive *Embryo*, and an attached basal part which remains filamentous. This is called the *Suspensor*, since it holds the embryo in a definite position during its early development, surrounded, and nourished by the semi-fluid contents of the enlarging sac.

THE EMBRYO.

Among Dicotyledons the embryo of *Capsella*, the Shepherd's Purse, in which the development was first followed out in detail,

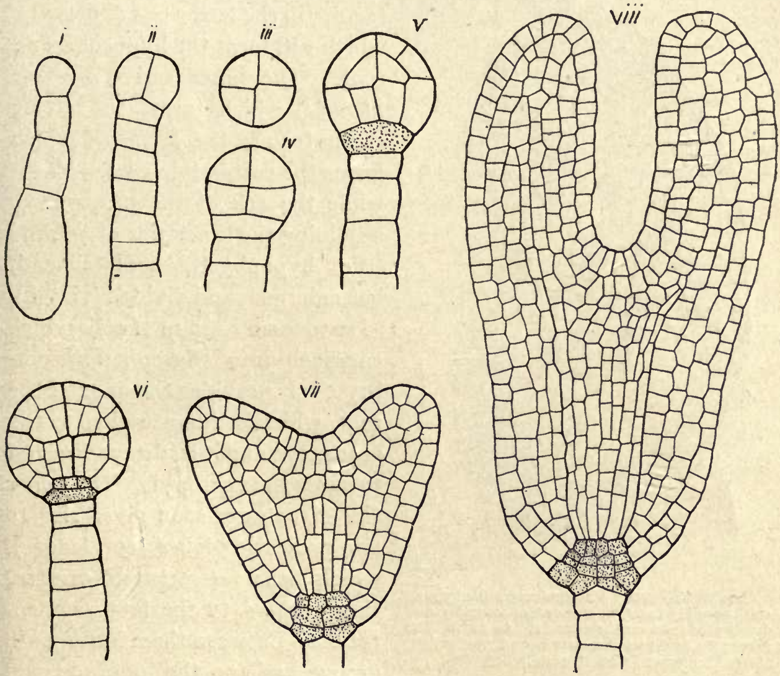


FIG. 217.
Embryos of *Capsella* in various stages of development. (i.-v. after Famintzin; vi.-viii. after Hanstein.) The hypophysis and its products are shaded. All these embryos have the apex upwards, and the root downwards. But it is to be remembered that the root always points to the micropyle of the ovule, as seen in Fig. 218.

serves as a very general type. The filamentous pro-embryo (Fig. 217, i.) has the cell at its basal, or micropylar end greatly enlarged. The cell at the apical end is relatively small at first, but it gives rise to the greater part of the embryo, a smaller part originating from the next lower cell. The apical cell enlarges into a spherical form, and divides into octants, by walls at right angles to one another and to the outer surface (anticlinal). Their position is uniform, and the first is usually longitudinal (ii.), but their succession may vary. This suggests that no great morphological value can be set on their order of appearance (iii. iv.). Later each octant divides into an outer and inner cell, by a wall parallel to the surface (periclinal); the superficial cells thereafter divide only by anticlinal walls, and the layer is called *dermatogen*, because it forms the epidermis (v.-viii.). The inner cells divide again periclinally to form an inner and an outer series; this is more regular in the lower tier of octants, which will form the hypocotyl and root. The inner series are the *plerome*, which forms the stele; the outer are the *periblem*, which forms the cortex (vi.-viii.). Meanwhile the cell of the pro-embryo adjoining the lower tier of octants (the hypophysis, here shaded) has enlarged, and divided (vi. vii.), so as to form a group of cells which encroach into the spherical embryo. It provides the apex of the root, which is thus attached to the suspensor, and it is always directed towards the micropyle. The upper tier of octants soon gives rise to two projecting lobes (cotyledons), which bear no constant orientation relative to the first segmentations. Between them is a smooth groove, where the plumule will arise later. It is now possible to recognise the position of all the parts of the germ, viz. the radicle, the two cotyledons, and the plumule between them. In the Shepherd's Purse the seed is exalbuminous (p. 281), and the embryo develops fast in bulk, and in length (Fig. 218). But the ovule is of the type with a curved embryo-sac. The embryo, as it grows, adapts itself by curving also, and soon fills the greater part of the sac. Meanwhile the plumule at last appears at the base of the groove between the cotyledons. Its position coincides with the intersection of the octant walls. Accordingly its position was

FIG. 218.
Shepherd's Purse. Photomicrograph of young seed, showing embryo, endosperm centrally, and developing testa on the outside. (× 125.) The micropyle is directed upwards and to the left. (After Coulter and Chamberlain.)

defined by the first segmentations of the zygote. Thus the embryo of a typical Dicotyledon springs from the two distal cells of the filamentous pro-embryo. The larger part, including the cotyledons, plumule, hypocotyl, and most of the root arise from the distal cell; the tip of the root originates from the cell next below it; the rest of the pro-embryo acts as an organ of attachment.

While the *Capsella*-type shows the embryogeny usual in Dicotyledons, aberrant forms are not uncommon. But as they are mostly sporadic in their distribution they do not suggest any consistent basis for morphological argument. It is rarely that a family includes many aberrant types: an exception is seen in the Leguminosae, where the peculiarities are most marked in the suspensor. Of the rest, the most interesting variants are the pseudo-monocotyledonous embryos. In certain plants that are clearly Dicotyledons in their general characters, only one cotyledon appears. This is seen in *Carum bulbocastanum*, *Eranthis hyemalis* and *Cyclamen persicum*; and it is probably due to abortion of one of the cotyledons. But in some cases it is believed to result from a lateral fusion of the two cotyledons to form one, as in *Ranunculus Ficaria*. Much other evidence suggests that the Monocotyledonous state is derivative from that of the Dicotyledons. This conclusion is further countenanced by the fact that occasionally Monocotyledons are found with two cotyledons (*Agapanthus*), or even four growing points may appear on a peripheral zone (*Cyrtanthus*). In such cases the apex of the axis would be central and terminal, as in the *Capsella*-type. But in most Monocotyledons it is lateral, as it is in *Alisma*.

The development from the zygote in *Alisma* or *Sagittaria* is typical for a large number of Monocotyledons. The first divisions give rise to a three-celled pro-embryo, of which the basal cell (*q*) is enlarged, and does not divide further (Fig. 219, i.). The middle cell divides into several cells (*m*, *n*, *o*, *p*, Fig. 219, ii.). The distal cell divides into quarters, and subsequently by anticlinal and periclinal walls so as to form the single terminal cotyledon (Figs. ii.-v., *l*). Meanwhile in the tier of cells below this (Figs. ii. to v., *m*) a lateral depression begins to appear, which develops into the apex of the axis. This is then lateral in origin, while the cotyledon is terminal. The hypocotyl and root-tip spring from the next two tiers (*n*-*o*, Figs. ii.-v.). It thus appears that the reference of the several parts to cells of the pro-embryo differs in the *Alisma*-type from that in the *Capsella*-type. The most remarkable difference lies in the lateral origin of the apex of the axis in *Alisma*, while in the *Capsella*-type the cotyledons are lateral, and the apex distal.

In a number of Monocotyledons the embryo differs from the *Alisma*-type. The most interesting are those in which the apex of the axis originates from the terminal cell of the pro-embryo. This occurs in the Dioscoreaceae and

Commelinaceae (Fig. 220), also in *Zanichellia* and others. There is reason to believe that the stem-tip in the embryo of the Monocotyledon was originally

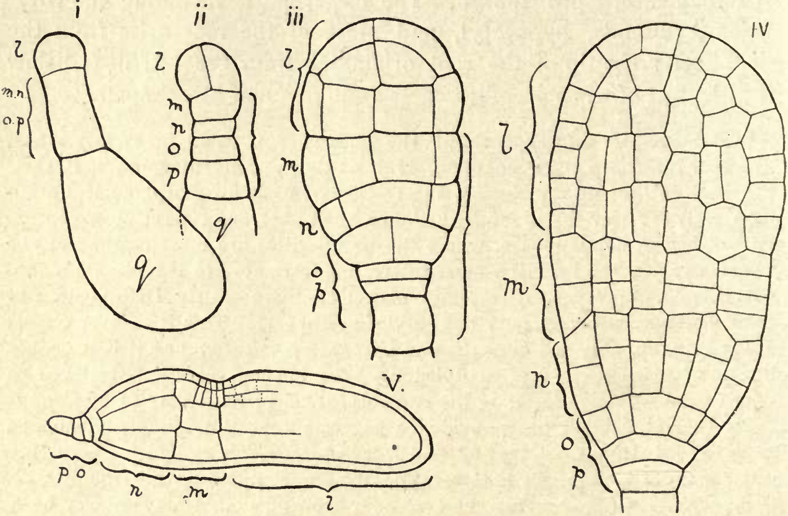


FIG. 219.

Successive stages of development of the embryo of *Alisma*, after Famintzin. *l, m, n, o, p, q* represent successive cells of the pro-embryo, and the tissues derived from them by division.

terminal, as in the Dicotyledons, but that in most types it has been forced to one side by the strong growth of the single cotyledon. If this were so the *Alisma*-type would be a derivative, and secondary condition, and an apparent anomaly would thus be explained. For among Vascular Plants the embryos of the *Alisma*-type are the only exceptions to the otherwise general rule; which is, that the apex of the shoot bears a constant and close relation to the centre of the distal tier of cells composing the embryo.

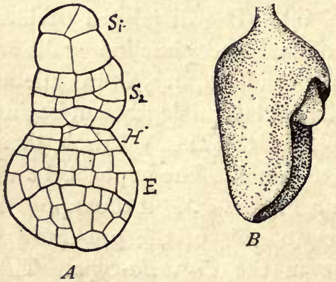


FIG. 220.

Embryos of *Tamus*. (After Solms-Laubach.) *A*, younger; *B*, older. s_1s_2=suspensor. *H*=hypophysis. *E*, body of the embryo. Here the embryology is more nearly of the type of *Capsella*.

The very peculiar structure of the embryo in Grasses has caused much discussion. The question has arisen whether or not the "scutellum," which faces the endosperm, and acts as a sucker from it, is or is not the cotyledon. The view now held as probable is that the cotyledon is highly specialised. A basal part of it appears as the scutellum, the distal part of it as the "cotylar sheath." The origin of the plumule appears here also to be from the apex of the embryo.

The three primary *antipodal cells* (*ant.* Fig. 206, p. 258) have no wall up to the time of fertilisation. Their subsequent behaviour is variable. Sometimes they are at once disorganised; but in most other cases they remain functional. They may grow to large size, as in many Ranunculaceae; or they may undergo fragmentation of nuclei, and even cell-division, so as to form a considerable tissue, as in the Compositae and other Gamopetals. Their use appears to be to act as intermediaries between the vascular supply and the enlarging embryo-sac, before the endosperm is organised as a tissue. To that end they sometimes develop as suckers penetrating the chalaza. But in any case they only help towards the final end, which is the full development of the germ.

The Endosperm.

The triple fusion, of the two polar nuclei with the second male gamete, has already been noted (Figs. 214, 216). The first division of

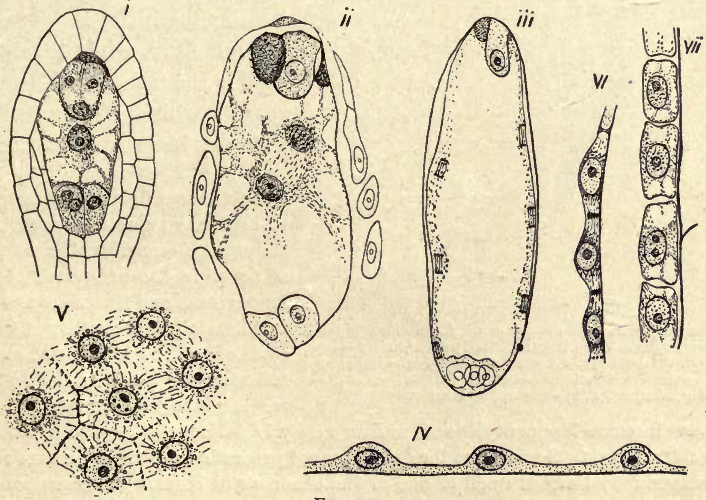


Fig. 221.
Successive stages of development of the endosperm in *Myosurus*. (After Strasburger.) (i.-ii. and iv.-vii. ×400; iii. ×170.) i. shows state at fertilisation. ii., embryo-sac much enlarged, and first division of the fusion-nucleus. iii. shows embryo-sac still more enlarged; it is on a lower scale of magnification. iv.-vii., stages of cell-formation round the numerous nuclei, derived by division from the fusion-nucleus.

the resulting triple-fusion-nucleus usually precedes that of the zygote (Fig. 221, i. ii.): it is repeated synchronously, in rapid succession, so that the numerous nuclei formed are found to be in corresponding stages of division, and their number at any moment is some power of two. Their chromosome-number is at first diploid, but the number is not strictly maintained. Meanwhile the embryo-sac grows rapidly, and the large central vacuole is surrounded by a thin peripheral film of cytoplasm, in which the free nuclei are embedded (Fig. 221, iii.-vi.). Partition-walls are formed later, isolating each nucleus in its own cytoplasmic area. Sometimes several may be present in a single cell, but when this is so they commonly fuse together. The embryo-sac is thus lined internally by a flattened layer of uni-nucleate cells, surrounding a large central vacuole (vii.). These cells then grow inwards, and divide, encroaching on the central cavity: this they ultimately fill with the compact tissue of the endosperm, which embeds the embryo. Sometimes, however, a central cavity may still remain. This is the case in the Coco-Nut, where the cavity is filled with the "milk," which is actually vacuole-fluid, while the white flesh is the tissue of the endosperm, which has not filled the very large embryo-sac.

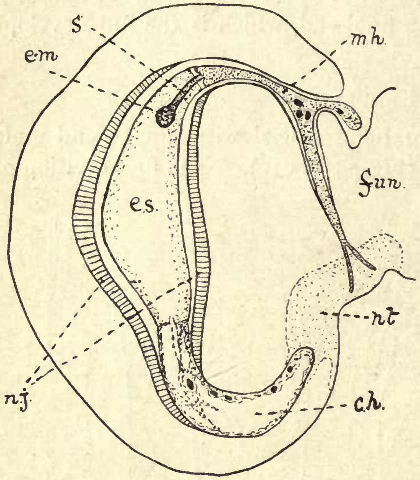


FIG. 222.

Median section of an ovule of *Rhinanthus minor*, showing haustoria. (After Balicka-Iwanowska.) *s* = suspensor. *em* = embryo. *e.s.* = embryo-sac. *fun.* = funiculus. *n.j.* = nutritive jacket. *nt.* = nutritive tissue. *c.h.* = chalazal haustorium. *m.h.* = micropylar haustorium.

The above description applies to ordinary types of ovule. But there is a considerable variety of detail in the behaviour of the embryo-sac and its contents after fertilisation. Frequently the first division of the fusion-nucleus is followed by a cell-wall dividing the sac into two chambers; this is seen in some Monocotyledons, and in many Dicotyledons, especially among the Gamopetals. Sometimes the development proceeds no further; but usually divisions may be continued in one or the other, or in both of the chambers.

More marked modifications are connected with the nourishment of the embryo-sac. In relatively primitive types like *Myosurus* the sac merely increases greatly in size, encroaching upon the surrounding tissues, which make way for it. Their cells collapse and their substances are absorbed into the growing sac, which acts thus parasitically upon them (Fig. 221, ii.). But in more specialised types, such as the Gamopetals, the nursing of the embryo-sac is more exact. They have only a single integument, while the sac so n crushes the small nucellus out of existence. The innermost layer of the integument then abuts on the growing sac, and forms an epithelial jacket of prismatic cells (Fig. 222, *n.j.*). This serves as a permanent nourishing tissue, which acts till the embryo-sac is well advanced.

In addition to this the embryo-sac itself may frequently put out local HAUSTORIA, which penetrate to favourable sources of nourishment. A good example of this is seen in *Rhinanthus* (Fig. 222), where, in addition to the epithelial jacket (*n.j.*), haustoria are formed at both ends of the sac. The chalazal end (*c.h.*) extends so as to reach a mass of nutritive tissue (*nt.*) close to the end of the vascular strand. From the micropylar end a similar haustorium passes through the micropyle, and traverses the funicle towards the same source of supply (*m.h.*). The haustorial connections may be still more elaborate in other plants (*Plantago*). Such arrangements indicate the importance of the nourishment of the sac, especially in its earlier stages. They also provide interesting analogies with the behaviour of parasites, whether in Fungi or in Flowering Plants.

The *function of the endosperm* is to provide temporary nourishment for the embryo which it surrounds. But the amount of the supply, and the time when it is yielded to the embryo may vary. Two main types of seed arise accordingly. In the first the embryo grows slowly, and keeps in close touch with the endosperm, which remains relatively large till the seed is ripe; it embeds the embryo and is stored with food. The result of this is the "albuminous" seed (p. 10). It is probably a relatively primitive state, and it is found in such families as the Ranunculaceae and Magnoliaceae, and in most Monocotyledons. Moreover, all Gymnosperms have seeds of this type. In the second the embryo develops more quickly. It absorbs the available nourishment early, so that at ripeness little or nothing remains of the endosperm. Its function has been temporary. Such seeds are called "ex-albuminous" (Fig. 226). Intermediate states are found, as in the Leguminosae, which, though usually held to be exalbuminous, have in many cases a band of mucilaginous endosperm covering the embryo (Fig. 224). While the substances stored in the endosperm provide for the further growth of the germ, they also supply the staple food of man in the various cereal grains.

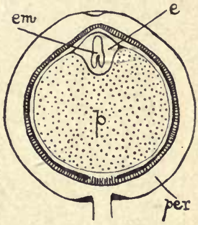


FIG. 223. Vertical section through a Peppercorn. *em*=embryo. *e*=endosperm. *p*=perisperm. The testa is shaded. *per*=pericarp. (After Baillon.)

In some cases the store of food for the embryo may in part be outside the embryo-sac, in the chalazal region of the nucellus. Such tissue is called *perisperm*, and it is found in the Peppercorn (Fig. 223), or the seed of the Water-Lily. The difference from an ordinary albuminous seed is morphological rather than physiological. But in the great majority of cases the nucellus is obliterated early, owing to the precocious growth of the megaspore which it envelops while young. Accordingly, it is not represented as a rule in the ripe seed, except by the remains of its tissue, which are crushed between the firm seed-coat and the endosperm or embryo within.

On the other hand, the integument, or integuments, persist, developing into the *testa, or seed-coat.* Their tissues become indurated, of stony or leathery texture; but there is a good deal of variety in the detail. Usually the outermost layer, but not infrequently some layer more deeply seated, develops its cells in prismatic form and thick-walled. Others may also harden: but the inner, softer layers are often compressed. The tissues lose their cell-contents, serving only the purpose of protection to the germ and the stores within. (Fig. 224.) When this condition is reached in many-seeded ovaries

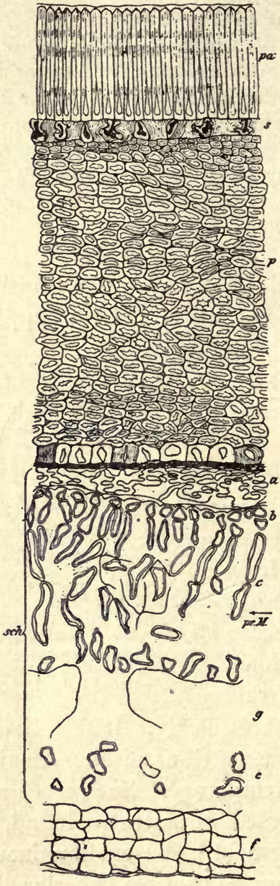


FIG. 224.
Section through testa, and mucilage-endosperm of seed of *Gymnocladus canadensis*. *pa*=palissade layer. *s*=supporting layer. *p*=thick-walled fissure. These form the testa. *sch*=mucilaginous endosperm of this Leguminous seed. (After Nadelmann.)

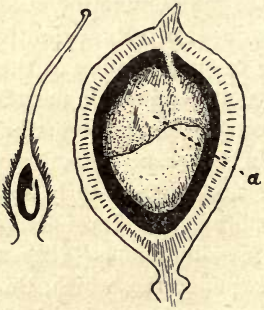


FIG. 225.
Young carpel, and fruit of *Copaifera*. *a* indicates the arillus which spreads from the micropylar end of the pendent seed. (After Baillon.)

the tissue of the funicle dries, and being brittle, the connection between the seed and the parent plant is severed. It is now independent, and the new individual has to fend for itself.

Other developments, having special biological value, are sometimes formed during the ripening of the seed. Superficial cells may grow into long *hairs,* as in the Cotton, Willow, or Poplar. These are effective in the transfer of the seed by the wind. Succulent bodies may sometimes be formed by local hypertrophy; such as the massive enlargement of the micropylar region to form the "caruncle" of the Spurges. A growth may proceed from the base of the ovule, appearing as an extra integument, or *arillus* (Fig. 225). The Mace sold by grocers is an example. It appears after fertilisation as a partial covering, highly coloured and strongly flavoured, round the true seed, which is sold as the Nutmeg. The bright orange sheath round the ripe seeds of the Spindle Tree are of the same nature. In both cases the aril is exposed as the fruit ripens, and its presence is believed to promote distribution of the seeds by Birds. But such developments are infrequent.

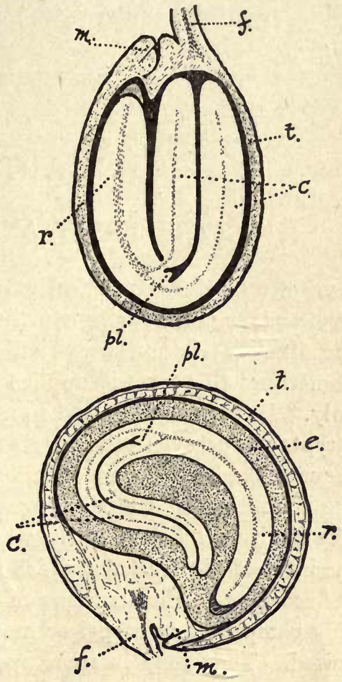


FIG. 226.
Seeds in median section: the upper (*Capsella*) exalbuminous, the lower (*Datura*) albuminous. f = funiculus. m = micropyle. t = testa. e = endosperm. c = cotyledons. pl = plumule. r = radicle. (Enlarged.) (Dr. J. M. Thompson.)

Each seed contains normally a single germ, together with a store of nutriment either in the germ itself or in the accessory tissues. (Fig. 226.) As it ripens it dries out. In this state, after separation from the parent it may undergo a period of rest. But sooner or later its function is to establish a new individual. In order that this may be most effectively done it is important that each seed should have the chance of independent development, a condition which is secured by dispersal of the seeds.

Each seed thus represents a single matured megasporangium, or ovule. It is a composite body comprising parts derived from three generations. The seed-coat, and the perisperm when present, consist of tissues of the parent diploid plant. The endosperm is usually held as representing, in a specialised and altered state, the haploid female prothallus, or gametophyte generation. The germ, which results directly from fertilisation, represents the new diploid generation. That these are all closely related in the seed of Flowering Plants is a late and derivative state, which cannot be properly understood till certain lower types have been described.

CHAPTER XVIII.

THE FRUIT AND SEED-DISPERSAL.

THE effects of Fertilisation extend in Flowering Plants beyond the ovule or megasporangium to the carpels, and often also to the floral receptacle. The mature Pistil or Gynoecium is called the *Fruit.* Sometimes this term is applied in a strict sense to the ripened pistil only. But it may be used in a more extended sense to include the receptacle, or even other parts when they also undergo changes consequent on fertilisation. This wider use of the term accords with the definition of the Flower as a simple shoot bearing sporangia. The Fruit would then be the whole of that simple shoot developed in the interest of the ovules which it bears.

According to the structure of the flower that produces it, the fruit may comprise one carpel or more. The carpels may be separate or united. They may in more specialised types be sunk down in the tissues of the receptacle. Such differences of the gynoecium existed already in the flower, and they remain as the fruit ripens, giving variety to the construction of its different types. It would be possible to analyse and describe the several kinds of fruits on the basis of their *morphological* structure, and it is necessary to do this when the chief purpose is systematic classification (see Appendix A). But another method is to examine them from the *biological* point of view. The function of the fruit is then taken as the basis of their study, and the attempt is made to see how each type is fitted for its performance. That is the aspect which will now be developed.

The functions of the maturing fruit are the *protection* and *nourishment* of the ripening ovules, and the *dispersal* of the seeds. It will not be necessary to dwell upon the first, for it is so obvious. In superior fruits the ovule, or ovules, are covered in by carpels, and attached to them by their funicles. In this way effective protection and nourishment are afforded during development. But they are still better secured in inferior ovaries; for in these the ovules are surrounded also by the massive tissue of the receptacle, while they are brought nearer to the source of vascular supply by their deeply sunken position. The protection becomes more effective as the maturing of the gynoecium proceeds, for its tissues frequently become more bulky and succulent. But still more is this so in others which harden with age. Extreme cases are seen in nuts or stone-fruits, where the woody tissues of the carpel reinforce, or sometimes mechanically replace the seed-coats. Since the seed with its nutritive store offers attractions to animals as food, the biological importance of such strong mechanical protection should be duly recognised.

But the biological fact which has dominated the evolution of the fruit, as regards its development after fertilisation, more than any other is the need for the dispersal of the seeds. The greater their number the greater is the need for it. Sooner or later each seed should have the opportunity of germination. This is carried out with the best prospect of success where each is isolated from its neighbours. Moreover, a wide dispersal leads to the spread of the species, and thus helps it in that competition for room in an over-crowded world which has been called the Struggle for Existence. The size of the individual seed is an important factor in the problem of dispersal. Clearly, the larger the seed the better is the chance of successful establishment of the young plant on germination; for the larger the store it carries with it the larger the vegetative system it will be able to form before it has to depend on its own resources. But the larger the seed the less easily will it be transferred from point to point. There are thus two conflicting factors of success. In the course of evolution plants have severally struck their own balance between these opposing factors, and the variety of fruit-construction shows in what different ways the problem may be solved. The success of each may be measured by the survival, numbers, and spread of those plants which have adopted them. These are the underlying conditions which should be kept in mind in studying the structure of the fruit, and its relation to seed-dispersal.

It is probable that a primitive type of gynoecium was apocarpous, containing a number of ovules. Such a carpel is seen in the pod of a Pea, or in the follicle of *Caltha* or *Aquilegia*. Along several lines of Descent comparison suggests that there has been a reduction in the number of ovules to a single one. This is illustrated in the Ranunculaceae. The Helleboreae have follicles and are probably a central type (e.g., *Helleborus, Aconitum, Caltha*, Fig. 227). In the carpel of *Anemone* only a single ovule matures, though several are initiated but remain vestigial (Fig. 228, *a*). In Rue and Buttercup only a single ovule is present (Fig. 228 *b*, 229). On the other hand, the number of carpels in the Helleboreae is about five; but a much larger number are present in *Anemone* or Buttercup; the more numerous carpels make up for the reduction of the ovules to one in each. Similarly in the Leguminosae a primitive type is seen, with many ovules in each carpel in the Pea or Bean. But *Copaifera* contains but two ovules, of which one only ripens into an unusually large seed (Fig. 225, p. 282). Again, in the Rosaceae, in *Spiraea* or *Cydonia* each carpel is many-ovuled; but in the Potentilleae, Rubeae and Roseae each has only one. The loss of number is, however, made up by the greater number of carpels. In the Pruneae, on the other hand, the single carpel contains two ovules, of which usually only one matures; but it grows into a large kernel. The

FIG. 227.

FIG. 228.

FIG. 229.

FIG. 227. Follicles of Aconite. (After Figuier.)
FIG. 228. *a*, Carpel of Anemone, with abortive ovules. *b*, Carpel of *Thalictrum*. (After Prantl.)
FIG. 229. Achene or nut of Buttercup. (After Figuier.)

gynoecium of the Oak is trilocular, with two ovules in each; but only one of the six ovules matures into the seed in the large acorn. The Coco-Nut again shows three loculi, but only one matures its single very large seed. A similar condition on a smaller scale is seen in Valerianaceae, while the gynoecium, with a single loculus and a single ovule in each flower, becomes the rule in the Teasels and Composites: these may be held to be examples of an extreme state.

Such evidence clearly indicates a progressive reduction in number of ovules produced and matured in the cases quoted. It often goes with increase in size of the individual seed, as in the Plum, Oak, and Coco-Nut, which gives greater certainty of successful germination. But some families show the converse, viz. that there has been a progressive increase in number of the seeds, though the individual size of the seeds is diminished. The most marked examples are seen where some irregular form of nutrition makes germination hazardous. For instance, in the mycorhizic Orchidaceae, where over a million seeds have been estimated as the produce of a single capsule. In many of the mycorhizic Ericaceae the seeds are numerous; and the same is seen in the parasitic Rafflesiaceae or Balanophoreae. In such cases the large number of seeds covers the risk of germination.

Such differences in number and size of the seeds must profoundly affect the mechanical problem of seed-distribution. The minute seeds of an Orchid can be scattered by a breath, but this would have no appreciable effect upon a Coco-Nut in its natural husk.

Dissemination of Seeds.

Seeds being themselves immobile require some agent outside themselves for their dispersal. Various means are effective. Partly the dispersal may be dependent upon the structure of the pistil, as in explosive fruits. But usually it is carried out by means of transfer outside the plant, such as currents of air, or water, or the movements of animals. There is an obvious analogy in this between seed-dispersal and the transfer of pollen. In both cases the immobile plant depends upon external agencies for transfer of essential parts. But the two present quite distinct problems. In pollination the end is to deposit the pollen-grains upon the stigma, and the more accurately this is done the better. In seed-dispersal the end is simply the wide separation of the individual seeds. Accuracy is of no importance.

In primitive types of fruit, as the carpellary wall matures, its tissues commonly become hardened. Where the seeds are numerous they require to be set free for germination. The natural course is by *splitting or dehiscence of the carpel*; and this is carried out in various ways. A split most naturally follows along the line of the coalescent margins of the folded leaf. This is the case in the follicle of Aconite (Fig. 227). A similar split may also sever the carpel at its midrib, as in the pods of Peas and Laburnums. The case of syncarpous fruits is not so simple. Their capsules open sometimes by longitudinal slits, as in *Cardamine* (Fig. 93) or *Hura* (Fig. 94), sometimes by transverse slits, sometimes by valves or pores: and this may occur either in superior or in inferior fruits. The seeds can thus escape, leaving the carpellary structure behind as an empty husk. On the other hand, in cases where the carpels are separate, and the number of the seeds in each is reduced to one, dehiscence is unnecessary, while the firm tissue of the carpel may form an additional protective wall. The resulting *achene*, or *nut*, is then shed bodily, as if it were a single seed, though it is strictly speaking a fruit. This is seen in the Buttercup, or *Potentilla* (Fig. 229). It may happen also in syncarpous pistils where only one seed matures, as in the Hazel, Acorn, or Coco-Nut. A peculiar case is that of the Umbelliferae, where the inferior ovary splits into two halves, each corresponding to one of its two carpels, and each containing a seed. Each half is practically equivalent to an achene (Fig. 432, vi., Appendix A).

To *release* the seeds as separate bodies is one thing, to *disseminate* them is a distinct proposition. By various modifications of the ripening pistil this second end may also be secured, sometimes by the activity of the pistil itself, but oftener through the medium of external agencies. The plant itself may disperse its seeds by means of various mechanical arrangements, which often result from the sudden release of strains set up in the capellary walls as they dry in the process of ripening. An instance is seen in the common hairy Cress (*Cardamine hirsuta*). Its fruit is the usual siliqua of the Crucifers; but the lateral valves, on splitting from their base, curl so sharply upwards that the seeds are forcibly thrown out (Fig. 93, p. 133). The method of the Geranium is similar, though differing in detail. Here only one seed is ripened in each of the five carpels. By sudden splitting from the base, and curling of the carpel upwards, the relatively large seed is slung out to a distance (Fig. 230). One of the largest and most effective of these explosive fruits is that of the Sand-box Tree (*Hura*, Fig. 94, p. 134). It is composed of 12 to 18 woody carpels, each containing one seed about ½ inch across. As the fruit hangs ripe upon the tree, the carpels suddenly split apart, and their woody shells take a twisted form, thus relieving the previous strains. By the sudden change the seeds may be thrown to a distance of some thirty yards from the tree. Another method is seen in the tricarpellary capsule of the Violet. When ripe the three carpels separate, and each boat-like carpel then presses its margins laterally together as it dries, and pinches the smooth seeds, which are thus shot out to a distance. Such examples illustrate the mechanical methods of dispersal seen in dry fruits.

FIG. 230.
Fruit of Geranium. (After Figuier.)

In some pulpy fruits the principle of the squirt is used. The fruit of the squirting Cucumber (*Ecballium*) hangs pendent as it ripens, and its outer pericarp is kept tense by the semifluid contents. When ripe it breaks away at the stem, opening a basal pore. As it drops the contents are sprayed out of it, seeds and all, to a considerable distance, scattering as they fall.

Dissemination by Wind and Water.

More frequently the motor impulse is from without, the chief agents being *wind*, *water* or some *moving animal*. Wind acts directly upon small seeds, such as those of Orchids, scattering them as it would so much dust. It may act less directly where the seeds are larger, and the dehiscent fruit is borne on a stiff stalk, as in the gaping follicles of the Aconite, which, shaken by the wind, scatter their seeds all round the parent (Fig. 227): or in the Poppy (Fig. 231) or Canterbury Bell, which do the same; but here the dehiscence is by pores, the principle being that of the Pepper-Box.

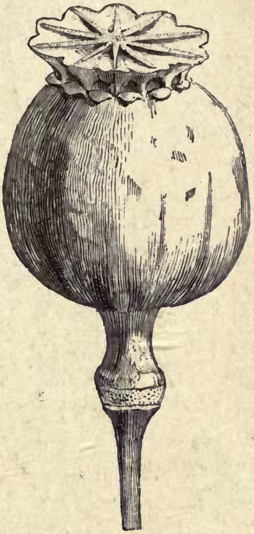


Fig. 231.
Capsule of Poppy opening by pores below the star-shaped stigma. (After Figuier.)

The wind would no doubt influence the fall of any seeds; but the development upon them of tufts of hair, or of broad thin wing-like surfaces, enhances its effect upon their transfer, even where the seeds are relatively large. Such developments are sometimes upon the seed itself, as in the case of dehiscent fruits: or they may be formed by the carpellary walls where the fruit is one-seeded, or where it breaks into one-seeded parts. The development of hairs on the seeds themselves is seen in the Willow and Poplar, in Cotton (Fig. 232), and in the

Fig. 232.
Seed of Cotton with superficial hairs. (After Figuier.)

Fig. 233.
Fruit of Valerian. (After Figuier.)

Willow-herb. When in any of these the fruit splits, the seeds are set free, each with its hairy parachute, which supports it in the breeze, so that it may be conveyed to a distance before reaching the ground. In many Valerianaceae (Fig. 233) and Compositae (Fig. 234), where the fruit is one-seeded and does not split, the calyx is persistent, and developing as the feathery pappus buoys up the inferior achene when set free, so that it may be conveyed to a distance before reaching the ground. The development of flattened wings upon seeds or fruits is closely analogous. Examples in the case of winged seeds are seen in the Bignoniaceae (Fig. 235), and of winged fruits in the Elm, Ash or Sycamore (Fig. 236). It is noteworthy that winged seeds and fruits are most common where the plants that bear them are of some stature, or are climbers; so that they have to fall a considerable distance. The wind has thus a chance of scattering them far and wide.

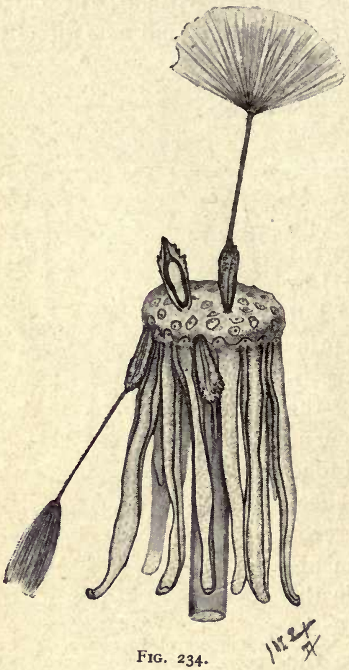


FIG. 234.

Fruit of Dandelion, with pappus as parachute. Note the absence of bracteoles on the general receptacle.

For large seeds a more effective means of transit is by water, which in commerce is a very efficient method for goods generally. Given a movement of water and a floating seed or fruit, dispersal is easy. The Water Lily is an example. The large berry ripens under water. It there splits, and the coherent mass of seeds, each with bubbles held in its aril, floats to the surface. There the seeds separate, drifting about till the bubbles are liberated by the decay of the aril. The seeds thus dispersed then sink. More striking examples are seen in littoral or estuarine plants, of which the seeds or fruits are often very large: for provided they float the size is immaterial. In *Barringtonia* (Myrtaceae), *Scaevola* (Goodeniaceae), and *Heritiera* (Sterculiaceae), which are all estuarine plants, the relatively large fruits have a fibrous

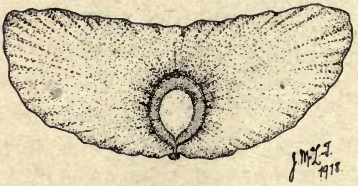


FIG. 235.

Winged seed of one of the Bignoniaceae. (Reduced.)

fruit-coat (pericarp), with air-spaces. Their large fruits can thus be easily floated away as they drop, by a stream or by tides. But

FIG. 236.
Samara, or winged fruit of Sycamore, dividing into two. (After Figuier.)

extreme cases are seen in *Nipa*, *Cocos*, and *Lodoicea*, all of them littoral and estuarine Palms. Their fruits have fibrous husks with air-chambers, and this serves to float them. Each contains a single

FIG. 237.
Fruiting annual plants of *Salsola*, caught at a wire fence, as they were rolled by wind over level sand, on the coast near Adelaide, Australia.

seed. Those of *Lodoicea*, the Double Coco-Nut of the Seychelles, are the largest known. They may be carried long distances by ocean currents.

Some plants show curvatures of the fruit-stalk, or of the shoot generally, which aid in the dissemination, or even in the exact deposit of the seeds. The fruit-stalk of the Ivy-leaved Toad-Flax directs its fruit to the crannies of the rock or wall in which it grows, so that its seeds are shed directly on the spot suitable for their germination. Some denizens of arid soil curl up their branches as they dry into a sphere, which when detached may be rolled great distances by the wind over flat ground, scattering their seeds as they go. This is seen in the "Rose of Jericho" and in the Grass, *Spinifex*. It is shown graphically in a species of *Salsola* which grows on the coast near Adelaide (Fig. 237).

Dissemination by Animals.

In various ways Plants may make use of the free movements of *animals*, which while serving their own ends become the involuntary agents of dispersal. The living seeds may be conveyed by them

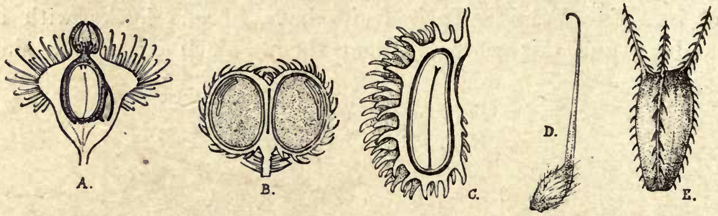


Fig. 238.
Fruits with hooked outgrowths, effective in transfer by animals. *A* = Agrimonia (Le Maout). *B* = *Galium* (Le Maout). *C* = Cynoglossum. *D* = Geum. *E* = Bidens.

externally, attached to their coats or other parts of their bodies: or internally, as ingested food: or they may be actually carried by them intentionally. For the first no special development is actually necessary in the seed or fruit. They may stick to the feet of animals clogged with mud, especially birds. Darwin removed the soil from the foot of an injured partridge, and obtained from it no less than 82 seedlings. But many fruits and seeds are provided with means of attachment; where the seeds are small, a sticky glandular secretion may serve, as in some Salvias. But many fruits develop as "burs," being provided with hooks of various origin, which attach them to fur or feathers. In the Burdock the tips of the bracts are hooked: in *Bidens* spines representing the calyx bear reflexed teeth (Fig. 238, *E*): in Cleavers (*B*), or the Carrot there are hooked emergences on the wall of the inferior ovary: in the "*Echinella*" section of the

Buttercups, or in the Hounds-Tongue (*Cynoglossum*) (*C*) they are on the superior achene: in the Water Avens (*Geum rivale*) (*D*) a single hook is formed half way up the style of each carpel. Such instances taken from different families, and involving quite different parts, show that these effective developments have originated repeatedly, and independently of one another.

FIG. 239.
Berries of the Currant. (After Figuier.)

A second and more prevalent means of dispersal is *internally*, as ingested food. It is secured by development of succulent tissues in close relation to the seeds. Here it is found that most various parts are involved, even in nearly related plants. Pulpy fruits occur in almost every family; even among the Grasses, which have characteristic dry grains, certain Bamboos bear a succulent fruit. The pulpy tissue often involves the whole carpellary wall, and the seeds are embedded in it: this is the case in the berries of the Grape, or Currant, the one being a superior the other an inferior ovary (Fig. 239). Or it may be only the outer part of the wall that is pulpy, while the inner is stony, as in the drupe of Cherries or Plums (Fig. 240). Sometimes parts other than the pistil itself may be involved, for instance the receptacle may be convex, and succulent, and bear the dry achenes (which are the true fruits in the restricted sense) upon its surface, as in

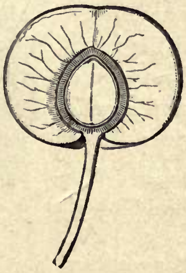


FIG. 240.
Drupe of Cherry. (After Figuier.)

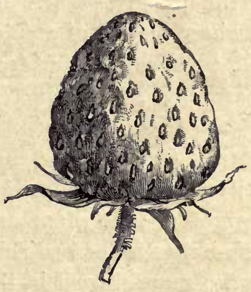


FIG. 241.
Succulent receptacle of Strawberry. (After Figuier.)

the Strawberry (Fig. 241.) Or it may be concave, and the achenes be borne within its hollow cavity, as in the "hip" of the Rose. In the Fig it is the massive axis of the condensed inflorescence that becomes concave and pulpy, while the achenes produced by the numerous flowers are contained within it (Fig. 242). Lastly, the perianth may be persistent, as it is in each of the aggregated flowers of the Mulberry, and becoming pulpy they embed the true fruits, which are achenes (Fig. 243). It is needless to multiply instances. Those quoted suffice to show how various are the parts that offer attractions by their succulent development to fruit-eating animals. Colour, scent, flavour and organic content, all attract them to these fruits as food. In the haste of feeding they do not exclude, but bolt the seeds, which may thus be carried by them internally to a distance before being voided with their *excreta.*

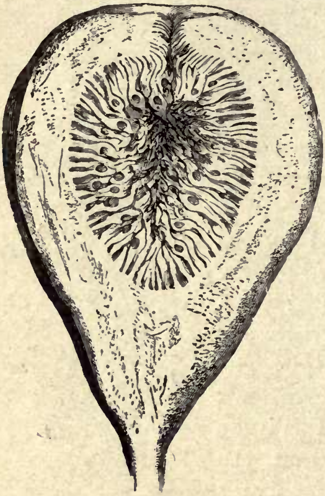


FIG. 242.
Succulent hollowed axis of the inflorescence of the Fig, bearing achenes within. (After Figuier.)

In these cases the animal is an unwitting agent. Another method, less effective but still to be reckoned with, is by means of intentional transfer of fruits or seeds for the animal's own purposes. Squirrels, some birds, and ants hoard stores of food in the form of nuts, etc.; sometimes the store is not fully exhausted, so that the live seeds germinate apart from the parent plant. But more exact results come where masses of esculent tissue, often containing oil, occur on the surface of the seed, in the form of caruncles, as in the Violaceae, Euphorbiaceae (Fig. 421 vii.-viii., Appendix A, p. 516), and Leguminosae. Observations have been made on the actual transfer of the seeds of Gorse by ants, and the spread of that plant on certain moor-lands can be definitely ascribed to this agency.

FIG. 243.
A "Mulberry" composed of many flowers, whose succulent perianths enclose each a dry achene. (After Figuier.)

Lastly, man himself is the most potent agent in the distribution of plants, though his influence is as often destructive as constructive. He consciously introduces plants of economic value to new areas, and clears off the native flora to make way for their cultivation. But he also unconsciously carries with him the seeds of certain plants, which appear as " weeds " wherever he goes. The

Nettle, the Shepherd's Purse, and the greater Plantain are the commonest of these.

All such devices for the dissemination of seeds as those described are to be held as offsets to the limitation imposed upon plants by their fixity of position. They are themselves immobile, as are also their seeds; but a spread of their seeds is essential for the survival of a species, or its spread to new stations. The measure of its success may be illustrated by a few examples. Darwin remarks that no cultivated plant has run wild on so enormous a scale as the Cardoon Thistle (*Cynara cardunculus*), introduced from Spain to La Plata. It has spread so as to cover large areas to the exclusion of other plants. Its "pappus" carries its fruits down the wind, after the manner of other Composites, and its spread shows the effectiveness of the method. A more recent example is that of *Lantana aculeata*, a native of Mexico, which was introduced into Ceylon as a garden plant in 1828, and has since spread all over the island, taking up waste land to the exclusion of other plants. It is spread by birds, which eat its pulpy fruits. Where forest fires occur in Canada the "Fire-Weed" (*Epilobium angustifolium*) at once occupies the cleared ground. It reaches the sterilised surface by its light seeds being supported in the wind by superficial hairs. A census was made some years ago of plants found growing in humus borne on the stumps of pollard Willows near Cambridge. The seeds or fruits from which they sprang would have had to be raised about eight feet above the ground. Of the total of nearly 4000 records, 44.62 p.c. were plants with fleshy fruits, 25.18 p.c. had winged or feathered fruits or seeds, 16.47 p.c. had burred fruits, 10.75 p.c. had seeds so light or small as to be easily wind-borne. Thus the presence of all the plants observed upon the stumps, excepting about 3 p.c., is accounted for by recognised methods of seed-dispersal. Such examples show the practical results of transport of seeds by the methods described, and give some idea also of the rapidity of their effects.

An experiment on the grand scale was made in the formation of a completely new Flora of the Island of Krakatau, and fortunately its results were followed by competent observers, who kept careful records. These form the best authenticated story of the natural formation of a plant-population in an area where none was living before. Up to 1883 the islands forming the small group in the Sunda Strait between Java and Sumatra, of which Krakatau is the largest, were covered by dense vegetation. From May to August of that year successive volcanic eruptions resulted in the complete sterilisation of the surface, which was covered with hot stones and ashes. Thus, on cooling an uninhabited desert was exposed, lying at a distance of fully twelve miles from the nearest vegetation. Since then a new Flora has sprung up upon the islands. This has been studied at intervals. The late Dr. Treub, who visited Krakatau in 1886, concluded that the first colonists were blue-green Algae associated with Diatoms and Bacteria. These formed a suitable *nidus* for the spores of Mosses and Ferns, and for the seeds of Flowering Plants adapted for dispersal by winds. On the beach were found the fruits and seeds of Flowering Plants carried by water, some of which had germinated; many of them belonged to the characteristic strand-flora of the Malay region. But the plants introduced by animals or by man were not found by him on this visit, which took place only three years after the eruption. In 1897 Penzig visited the island, and estimated that of the Flowering Plants noted 60.39 p.c. had reached it by ocean currents, 32.07 p.c. by wind agency, and only 7.54 p.c. had been transported by fruit-eating animals and man. On a subsequent visit by a party of botanists in 1906, the results as stated by Ernst show that though these proportions for Flowering Plants were not exactly maintained, still the largest number were borne by water-transit, and the smallest by animal agency. Thus for an oceanic island the most effective agency of transit is water; wind-carriage takes a middle place, and transit by animal agency is the least effective of the three. These are the results which would naturally have been anticipated.

Plant-Population.

A very important factor in the maintenance and spread of a species is the actual number of germs produced. The third Chapter of Darwin's *Origin of Species* deals with the geometrical ratio of increase of living things. Following Malthus he there points out that there is no exception to the rule that every organic being increases at so high a rate that, if not destroyed, the earth would soon be covered by the progeny of a single pair. Linnaeus had already calculated that if an annual plant produced only two seeds, and their seedlings next year produced two, and so on, then in twenty years there would be a million plants. This is, however, a very slow rate of breeding. The following table gives the results of careful computation by Kerner of the number of seeds produced in a single season by an average specimen of each:

Henbane (*Hyoscyamus niger*) - - -	10,000
Radish (*Raphanus Raphanistrum*) - -	12,000
Plantain (*Plantago major*) - - - -	14,000
Shepherd's Purse (*Capsella bursa-pastoris*) -	64,000
Fleabane (*Erigeron Canadense*) - - -	120,000
Tobacco (*Nicotiana Tabacum*) - - -	360,000
Flixweed (*Sisymbrium Sophia*) - - -	730,000

The Orchidaceae are extreme cases of productivity: the estimates of seed-production in them are as follows:

	Per Capsule.	Per Plant.
Cephalanthera - - -	6020	24,080
Orchis maculata - - -	6200	186,300
Acropera - - - -	371,250	74,000,000
Maxillaria - -	1,756,440	

Such figures convey little more than a general impression of vastness: but evidently the number of germs produced is far in excess of the actual requirement to make up directly for losses by death. There is in fact an immense margin, which may be regarded as a very efficient reserve to meet all the contingencies involved in the establishment of the germ till it reaches propagative maturity. Such a reserve is necessary, for the risks of youth are great. Many seeds fall victims to the predatory attacks of animals, which naturally divert to their own uses the food-stores laid by for the germ. Many never reach a situation fit for their germination. Many young plants are killed off almost at once by unfavourable conditions, such as unsuitable temperature, or drought, or unseasonable changes while in the defenceless condition of the seedling. Competition with the same or other races of plants destroys others. Fungal attack also takes its toll, and especially in the seedling state. But notwithstanding the number, and insistence of these risks, an overplus remains in any surviving species. This not only keeps the race in being, but in most cases provides for its spread into fresh areas, where, however, it is liable to be checked by various limiting factors. Moreover, the large numbers, and the competition which necessarily follows, provide material for Natural Selection to work upon: and it is the fittest that will be the most likely to survive.

Latent Period.

After seeds are shed and distributed they usually undergo a *period of rest.* During the autumn and winter of temperate climates they become buried in the soil. They naturally fall into chinks and crannies, and are often covered by rotting leaves; they are also washed into the soil by rain, or drawn below by the restless activity of earthworms, or covered by their castings. But some work their own way into the soil by hygroscopic movements, as in *Avena*, or *Stipa,* or *Erodium.* A few even bury their fruits as they mature by geotropic curvature of the fruiting stalk, as in the Earth-Nut (*Arachis*), or the subterranean Clover. In one way or another they become covered, and in the dormant season there is plenty of time for the process.

A latent or resting period is commonly determined by climatic conditions of drought in the tropics, or of cold in temperate climates. But a latent period may be *imposed* by the seeds themselves refusing to germinate till after a period of rest. In this respect seeds vary. Some will germinate immediately they are matured if the conditions are favourable. It is this that makes the difficulty with cereal crops in a warm, wet autumn : for those conditions stimulate immediate germination, and the corn is liable to sprout in the stook before it can be harvested. But as a rule a period of rest follows on ripening. The seed dries out, and in that state it remains stationary, but retains its vitality, being specially resistant to extremes of drought and heat. An example of an obligatory resting period is seen in the Sycamore. If the seeds are collected in autumn, and exposed to conditions favourable for germination, they remain passive till the spring, when they will all germinate almost simultaneously. The seeds of the Ash and the Hornbean are said to remain dormant two years, and longer periods are recorded for other plants. Others again have, in addition to seeds that germinate in the first year, others which require a longer rest : Laburnum, wild Mignonette, and field Clover are among these, while the Cockleburr (*Xanthium*), with its two fused fruits, is also said to germinate one in the first, the other in a later season.

Akin to such questions is that of the length of time during which seeds can retain their vitality. This varies in the individuals of any sample of seeds saved under apparently uniform circumstances. As the period is lengthened the proportion of seeds that germinate diminishes. Speaking generally, oily seeds retain their vitality a shorter time than starchy seeds ; and those kept dry retain it longer than those kept damp. Breaking up permanent pasture, or clearing old woodland gives results that indicate that seeds which had long lain dormant germinate when the conditions suit them. For instance, in a given case, the removal of 46 year old forest from land that had previously been cultivated resulted in field-plants springing up, presumably from dormant seeds. But to extend this possibility of survival to the so-called "mummy-wheat" is too long a step to seem probable. A. de Candolle, after examining the evidence up to 1882, concluded that no grain taken from an ancient Egyptian sarcophagus and sown by horticulturalists has ever been known to germinate. It is not that the thing is impossible ; but as a matter of fact the attempts at raising wheat from these ancient seeds have not been successful. The grain known in commerce as mummy-wheat has never had any proof of antiquity of origin.

Cycle of Life.

The germination of the seed, and the re-establishment of the sporophyte as its result, completes the normal cycle of life of the Flowering Plant. The leading incidents of that cycle may be represented by a diagram, which will serve later as a means of ready comparison with types of vegetation lower in the scale (Fig. 244). It will be found in them all that the leading events succeed one another in a sequence that is uniform, however different the details may appear. Two critical points in the cycle are marked by the fact that the

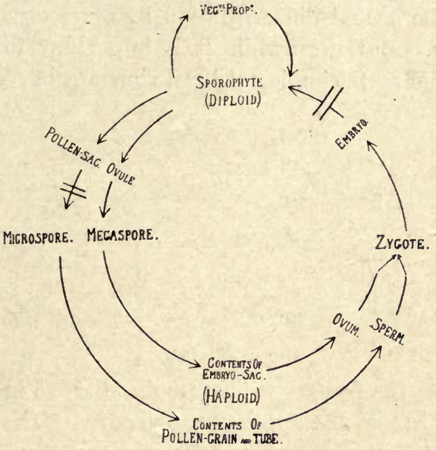


Fig. 244.

individual life is there presented in each case by a single cell. They are the *Spore* and the *Zygote*: the former follows on reduction, and is haploid; the latter results from fertilisation, and is diploid. Between these, and derived respectively from them, are two phases of cellular amplification, so as to form a soma, or plant-body. The one is the *Sporophyte* or rooted plant, which springs from the Zygote, and is diploid; the other is rudimentary in the Flowering Plants, though it is more fully represented in lower forms. It is initiated by the haploid spore, and is itself haploid. It consists here of only a few cells contained on the one hand in the embryo-sac, on the other in the pollen-grain and tube. It is called the *Gametophyte*. These two phases together constitute the alternating Cycle of Life of the Flowering Plant, which thus shows an *Alternation of Generations.*

The succession of events may often be obscured by vegetative propagation. But, as shown in Chapter XII., this is a mere process of extension, or repetition of the individual sporophyte. It appears as though it extended the cycle, but it does not really introduce any new feature. It may be fitly represented as a supplementary cycle outside the main diagram (Fig. 244).

The doubling of part of the main cycle indicates sex-differentiation, the male and female developments running parallel. This is a feature which is very prominent in Flowering Plants, and for them the cycle is thus doubled for about three-quarters of its extent. It will be found on applying a similar method successively to plants lower in the scale that in them the sexual differentiation becomes progressively a less marked feature. But meanwhile it is important to note that the extent of this differentiation is not itself constant in Flowering Plants.

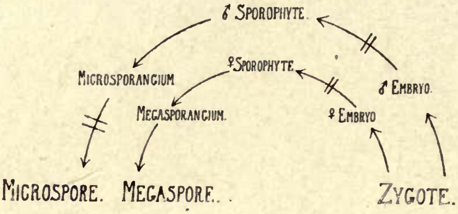


FIG. 245.

In certain plants the flowers are hermaphrodite, as in the Buttercup. The diagram as in Fig. 244 applies to such cases. The sex-differentiation appears in them only on formation of the pollen-sacs and ovules, which are in the same flower. But in others the plant is itself either male or female, and the species dioecious, as in the Willow. This condition may be represented by an amendment of the diagram as in Fig. 245. There may be various steps in this further sexual differentiation. For instance, in *Lychnis dioica* (Fig. 184, p. 236), which is descended from an hermaphrodite stock, the sex-difference appears to be decided by nutrition of the individual, rather than determined in the seed itself. But it is not improbable that in other cases sex may be determined by factors operating directly on the zygote. For us here the point of importance is this. That the stage at which difference of sex is first recognisable in the individual life is not fixed for all Flowering Plants. In hermaphrodite plants it appears only in the several organs of the individual flower. In dioecious plants the difference extends to the whole sporophyte plant. These observations will be of value for comparison with forms lower in the scale of vegetation. But such questions cannot be fully treated till these organisms have been described. Nor can the origin and real nature of that complex body, the seed, be properly understood till it can be examined comparatively. A knowledge of the propagative methods of more primitive plants must first be acquired; and the comparisons which follow from it will be taken up in a later chapter.

DIVISION II.

GYMNOSPERMS.

CHAPTER XIX.

CONIFERAE: THE SCOTS PINE.

So far the description which has been given has related to the Angiosperms, in which the ovules are protected by a carpellary wall, and the pollen-grain is received upon a stigmatic surface. These Plants appeared relatively late in Geological Time. Their records date back only to the Cretaceous Period. Comparative evidence supports the conclusion that they are the culminating types of Vegetation, and rightly occupy the highest position. Their ready adaptibility to their surroundings has led to their success in the struggle for existence, as shown by the profusion of their forms now living. In fact, they are the dominant types of the Present Day.

But Seed-Plants of a more primitive type long ante-dated the Angiosperms. Seeds existed in the Devonian Period. They belonged to forms corresponding more nearly to those living Plants which are collectively named *Gymnosperms*, than to the Angiosperms. This gives a special interest to the study of the living representatives of the Gymnosperms, a class which have as their leading characteristic the *free exposure of their seeds*, a carpellary protection being absent. The leading family of living Gymnosperms is the *Coniferae*, so named from the fruiting body with its hard woody scales, well exemplified by the ordinary *Fir-Cone*. Vast forests of such Conifers exist in temperate and sub-arctic zones. These are the sources of the supply of soft-wood, turpentine and pitch.

In the British Flora the Gymnosperms are represented only by Coniferae, such as Scots Pine (*Pinus sylvestris*), the Yew (*Taxus baccata*), and the Juniper (*Juniperus communis*); but many more are familiar in cultivation in shrubberies and woods. Over the world at large they include a number of other forms, somewhat loosely related, but with common features that indicate their primitive character. Among them are some of the largest and oldest of living organisms, such as the Big Trees of California (*Sequoia*, see Frontispiece). Another well-known and peculiar form is the Monkey Puzzle (*Araucaria imbricata*).

The seed of the Scots Pine, and other Conifers, produces on germination a seedling with a dominating main axis, which grows upright, and keeps as a rule its radial construction. Radiating groups of branches are borne at intervals upon it, which take a more or less flattened form; and as they do not grow so strongly as the main stem the result is the pyramidial habit so well seen in the Christmas Tree (*Picea*) and in the young Scots Pine. Sometimes this habit is maintained throughout life; but often, as in the Scots Pine, the form becomes irregular as the tree grows older. The Coniferae are as a rule closely gregarious, and they then form very exclusive forests. The lower branches die off in the crowded woods, giving the clean trunks without knots that are specially valued as timber.

The Scots Pine, like most of the family, is characterised by leaves of relatively small size, simple form and stiff texture. These are xerophytic features, and are well illustrated by the "needles" of the Pine. Their structure, with sunken stomata, a well-developed cuticule, and a large proportion of bulk to surface bears this out. Hairs are absent from their smooth surfaces. (Fig. 246.)

In some of the Coniferae the vegetative leaves are all of essentially the same type, as in the Juniper. But in the Scots Pine some of them are developed as protective scales, others as green foliage leaves, and the mutual arrangement of these two types is very characteristic. It is closely connected with the fact that all the axillary buds do not develop alike. Those at the end of the annual increment of growth are unlimited, and form the radiating group of branches of each successive year already noted. Those lower down develop only as limited *foliage spurs*, which remain short, bearing only a few membranous scales, and distally two long green "needles" (Fig. 246). In the seedling plant green foliage leaves may follow the cotyledons on the main axis. But in the later stages the main axis and the woody branches bear only scale-leaves, while the green needles are always borne on the foliage spurs. In the different species of *Pinus* the number of needles on each spur varies: in *P. monophylle* it may be only one. The Coniferae are mostly evergreens like the Scots Pine, Yew, and Juniper. But some, like the Larch, shed their leaves in autumn, or even their short leafy shoots, as in *Taxodium*.

The root-system starts in all cases with a tap-root; but it seldom maintains its lead. Lateral roots arise from it, and they form the chief attachment of the mature tree, which is often shallow-rooted. Some of them, as in the Scots Pine, are mycorhizic, the roots being invested by a fungal felt, which acts as an intermediary between the root and

FIG. 246.

Branch-end of *Pinus Laricio*, var. *Austriaca*, bearing laterally two shoots of unlimited growth, and a cone replacing a third one. Each is covered by numerous "foliage spurs" bearing two "needles." At the base of the figure these are fully developed; above they are half-grown, the shoot having been cut in spring. Two young female cones (♀) at the distal end, are at the period of pollination. (After Groom.)

the soil (p. 195). But as seedlings can be raised in pure cultures without the fungus, its presence, however advantageous, is not necessary.

The external characters of the Coniferae thus briefly sketched stamp the appearance of most of them. The general plan of their Plant-Body or sporophyte is the same as that seen in Angiosperms.

It is the working out of the details that gives the special characters of the Coniferae. Their habit is easily distinguished from that of the broad-leaved Dicotyledons, and still more easily from the Palms and other large Monocotyledons. A feature which has its bearing upon the habit and spread of the family is the rarity of vegetative propagation. This is in marked contrast to the Angiosperms. In Nature it hardly ever occurs, and the forester finds it impracticable. Virtually all individuals are raised from seed.

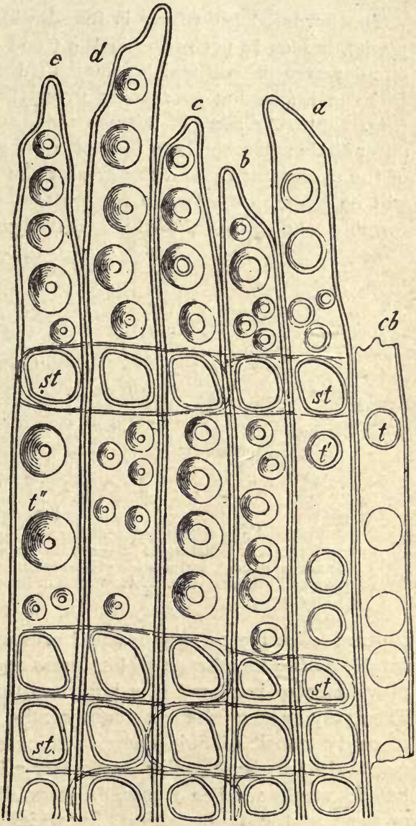


FIG. 247.

Tracheides of Pine, seen in radial section. *a-e*, are successive tracheides of one radial row. *cb*=cambium. *t*=young pit of cambium. *t'*, *t"*=older pits. *st*=pits of larger area facing the oblong cells of the medullary ray. (× 550.) (After Sachs.)

There is no need to describe the structure of the vegetative organs in detail, since they correspond in essentials to what has been seen in Angiosperms. It must suffice to note certain features of comparative importance. The stem is constructed on the same plan as that of the woody Dicotyledons, with indefinite secondary thickening of the vascular ring originating from a cambium (compare Fig. 34, p. 48). It results in the Scots Pine in a woody trunk marked by annual rings and medullary rays, while externally are phloem and a scaly fissured bark (see Fig. 39, p. 53). *Resin-passages* permeate all the tissues irregularly. They are specialised intercellular spaces, lined by an epithelium, which deposits the sticky resin in the passages. It exudes from them under pressure of the surrounding tissues whenever the plant is broken or cut. The most notable structural feature is that the *wood is composed entirely of tracheides*, each developed after tangential division from a single cambial cell (Fig. 247). They are arranged, as the cambium is, in radial rows, not disturbed as the wood of Dicotyledons is, by sliding growth, or unequal development of the individual cells. The wood is consequently of that even texture seen in "deal." The tracheides are lignified, and their radial walls are marked by *circular bordered pits.*

The bordered pit which is found widespread in the tracheae of vascular plants, is seen in perfection in the wood of Conifers. The pit originates as a circular area of wall which remains thin, while the rest of the wall thickens. But the thickening encroaches upon the area of the pit, and overarches it (Fig. 248). As seen in surface view a double outline then appears. The outer circle corresponds to the area of the pit-membrane, the inner to the limit of the overarching; and the greater the thickening the further these outlines will be apart. Meanwhile the centre of the pit-membrane itself thickens, forming the "torus," which serves mechanically to meet the risk of

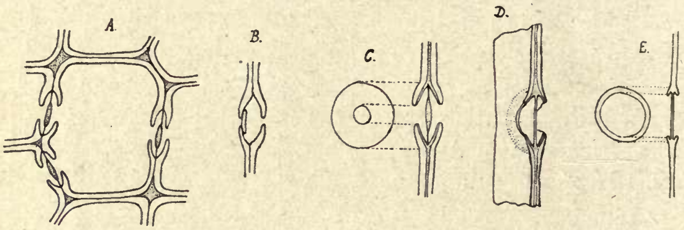


FIG. 248.

Bordered pits of tracheides of Pine. *A* = a whole tracheide in transverse section with pits in its radial walls. *B* shows the torus pressed to one side. *C, D, E* illustrate the development, and relation of the structure as seen in section to the double outline as seen in surface view. *E* shows this in the young state. *D* rather more advanced. *C*, mature.

rupture following on any unequal pressure on the two sides. For the torus would, as the membrane yields, press against the overarching lip (*B*). The prevalence of bordered pits indicates that they are functionally important. They may be recognised as a compromise between the conflicting requirements of ready transit of fluid between thick-walled cells and the maintenance of mechanical strength. For the former a large pit-membrane is an advantage, but it would weaken the wall. This difficulty is met by the overarching as seen in the bordered pit, by which the strength of the woody wall is maintained.

The phloem is also arranged in regular radial rows. It consists chiefly of *sieve-tubes* (*v*, Fig. 249) without companion-cells. They have cellulose walls and sparing contents. Cells of phloem-parenchyma are also present. The sieve-pits (*vt*) are mostly on the radial walls, and thus correspond in position to the bordered pits in the tracheides. The secondary tissues are traversed by medullary rays, as in Dicotyledons (Fig. 249). They include cells that retain their protoplasm, while minute intercellular spaces pass radially inwards between their cells. They serve accordingly for radial ventilation, as well as for storage within easy reach of the conducting phloem. Though the plan of construction of the vascular tissues of Gymnosperms is the same as in Dicotyledons, the details of their development are not so elaborate.

The chief comparative interest of such a plant as the Scots Pine lies not so much in the form and structure of the sporophyte-plant, as in the details of its propagation. This is carried out, as in the Angiosperms, by organs grouped as *Flowers*, which are *male* or *female*. In the Scots Pine these may be borne on the same tree, though often on distinct branches. The female flower, pink and succulent at pollination, matures into the hard *woody cone*, from which the name

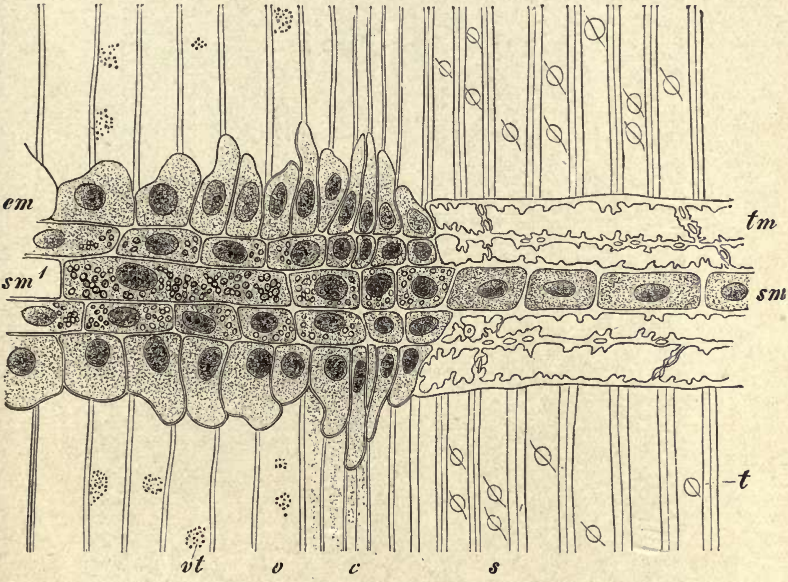


FIG. 249.

Radial section of Pine stem, at the junction of wood and bast. Phloem to the left, xylem to the right. *s*=autumn tracheides. *t*=bordered pits. *c*=cambium. *v*=sieve-tubes. *vt*=sieve pits. *tm*=tracheidal medullary ray cells. *sm*=medullary ray cells in the wood containing starch. *sm'*=the same in the bast. *em*=medullary ray cells with albuminous content. (× 240.) (After Strasburger.)

Coniferae is derived (see Fig. 246, p. 304). When ripe it consists of a central axis bearing in a complex spiral numerous woody *ovuliferous scales*. As the cone ripens the scales turn back, and two seeds may be seen freely exposed on the upper surface of each. When fully ripe each seed separates from the scale, together with a thin film of superficial tissue, which on detachment helps to float it away on the breeze. The seed is protected by a seed-coat, covering a bulky endosperm, with a large embryo enclosed in it, which has many cotyledons, plumule and radicle. The seed is thus "albuminous," and in essential points it corresponds to that of Angiosperms. But in the Scots Pine it takes two years to produce, and the details of its production give important features for comparison.

FIG. 250.
Pinus Laricio, var. *austriaca*. Shoot bearing male flowers in place of foliage-spurs. (After Groom.)

Both the flowers are axillary in their origin. The male flowers are produced in large numbers, replacing the weak foliage spurs (Fig. 250). The female take the place of the stronger branches of unlimited growth, and are produced in smaller numbers (Fig. 246). As they project upwards at pollination at the end of the extending shoot, they are in the best possible position for receiving the wind-borne pollen. The *male flower* is enveloped below by membranous scales, and bears distally numerous *sporophylls or stamens*, each with two pollen-sacs on its under side (Fig. 251, *B, C*). The pollen-grains are peculiar in bearing right and left of the grain itself air-containing sacs (wings), which give a low specific gravity to the whole grain, and so aid its transfer by the breeze (Fig. 251, *D*). At the time when it is shed, the grain of *Pinus* contains, in addition to the vestigial remains

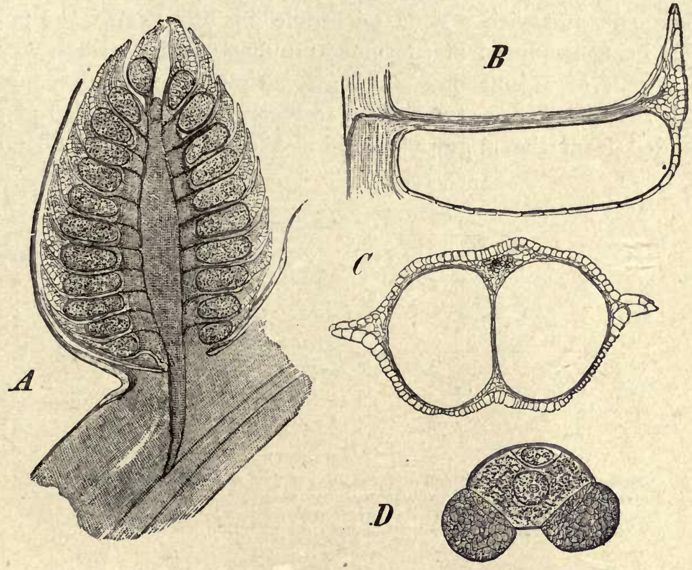


FIG. 251.

Pinus montana. A longitudinal section of a ripe male flower (× 10). *B*, longitudinal section of a single stamen (× 20). *C*, Transverse section of a stamen (× 27). *D*, a ripe pollen grain of *Pinus sylvestris.* The obliterated prothallial cells are not shown. (× 400.) (After Strasburger.)

of two obliterated cells of the male prothallus, one nucleated cell attached laterally (the *generative cell*), and a free nucleus (the tube nucleus) enclosed in cytoplasm which fills the rest of the grain.

The male flower is thus a simple shoot bearing sporangia. The *female flower* may also be regarded as a simple shoot. It consists of an axis bearing numerous scales that are at first succulent, but finally woody. They are arranged on a complex spiral plan. One of these scales removed from the young pink cone at the stage of pollination shows a double structure. A smaller lobe, sometimes called the *bract-scale*, bears on its upper surface a larger and thickened lobe, sometimes called the *ovuliferous scale* (Fig. 252). It seems probable that this is a local upgrowth of tissue from the surface of the former, though as the cone grows older it becomes woody, and is by far the more prominent feature of the two. Other interpretations of the cone have been given; but if this view be accepted, then the whole cone is a simple flower bearing many complex sporophylls. Attached to the upper face of the ovuliferous scale are *two ovules*, with their wide micropyles directed downwards. Each ovule consists of a nucellus corresponding to that of the Angiosperms, surrounded by a single integument, and with a wide micropyle (*m*, Fig. 252). The pollen-grains being produced in enormous numbers, and floating away on the dry air of a June day, are scattered over the female cones, of which the scales then stand apart to receive them. A drop of fluid extruded from the micropyle catches them and is then absorbed.

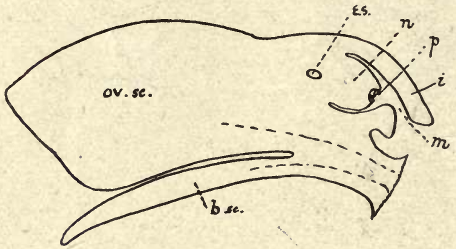


FIG. 252.

Median section of ovule and scales in Pine at time of pollination (after Coulter). *b sc*=bract scale. *ov. sc*=ovuliferous scale. *n*=nucellus. *i*=integument. *m*=micropyle. *e.s.*=embryo-sac. As the two ovules lie side by side, only one of them is seen in the radial section. *p*=pollen-grain or nucellus.

Thus *the pollen-grains are landed directly on the apex of the nucellus*, where they are constantly to be found in sections cut through the ovule (*p*, Fig. 252). Excepting that there is no receptive stigma the process is not unlike that in wind-pollinated Angiosperms.

But differences of great comparative interest lie in the details within the ovule itself. The ovule originates as in Angiosperms, and as in them the embryo-sac is one cell of a tetrad produced in the young nucellus; its nucleus is therefore haploid. But an essential difference is that in *Pinus*, and all other Gymnosperms, nuclear division proceeds to a high number in the young embryo-sac. Cell-formation follows, and *the sac is thus filled before fertilisation by a bulky tissue of the endosperm, or female prothallus* (Fig. 253). At the time of fertilisation, which in *Pinus* and *Picea* happens about the middle of June of the year after pollination, the female prothallus bears at its micropylar end three to six large *archegonia*, of which two commonly appear in a median longitudinal section of it (Fig. 253, *a*). Each of these originates from a single superficial cell of the prothallus, and consists of a large nucleated *ovum*, with a small lenticular *ventral-canal-cell* lying above it, which is cut off from the ovum shortly before fertilisation. Covering this is a group of cells two or more tiers in depth, forming the channel of the neck (Fig. 254, *A*). The ovum of *Pinus*, as is not uncommonly the case in Gymnosperms, is large

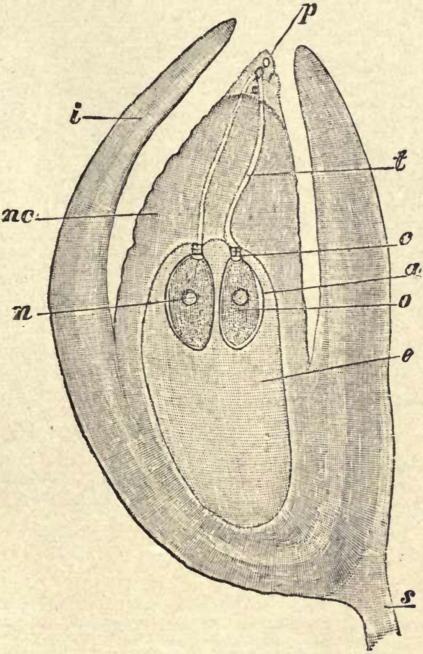


FIG. 253.
Median longitudinal section of an ovule of *Picea excelsa* at time of fertilisation. *e*=embryo-sac filled with tissue of the female prothallus. *a*=archegonium, showing venter (*a*) and neck (*c*). *n*=nucleus of ovum. *nc*=nucellus. *p*=pollen-grains. *t*=pollen-tube. *i*=integument. (×9.) (After Strasburger.)

enough to be seen with the naked eye. The archegonia lie in a slight depression of the surface of the prothallus. The last step before fertilisation is the collapse of the ventral-canal-cell, which takes no direct part in propagation.

In the Scots Pine a whole year elapses between the pollination of the young pink cone and the act of fertilisation. But in Conifers generally the times are different. With or without a lengthened interval each pollen-grain, germinating on the apex of the nucellus, forms a pollen-tube, which penetrates the nucellus, passing towards the apex of the prothallus (Fig. 254, *C*). Meanwhile its generative cell has divided to form a stalk-cell and a body-cell. The former breaks away from its attachment, and the contents of the grain enter the tube. The body-cell divides during transit to form the *two male gametes*. Thus provided, the tube enters the neck of an archegonium, and the gametes are transferred into the ovum. The nucleus of one of the gametes fuses with the nucleus of the ovum. The result of the fusion

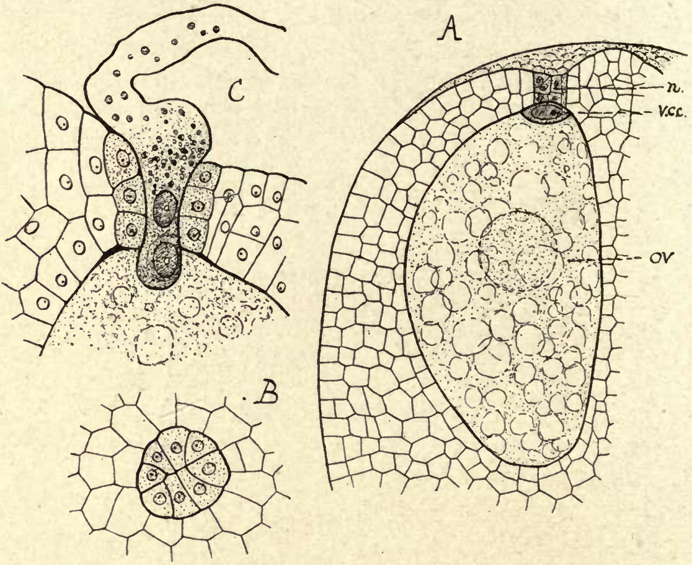


FIG. 254.

Picea vulgaris. *A*=longitudinal section through apex of female prothallus, and one archegonium. *n*=neck. *v.cc*=ventral canal cell. *ov*=ovum. *B*=neck seen from above. *C*=entry of pollen-tube with gametes into the canal of the archegonium. (*A* × 100; *B*, *C* × 250.) (After Strasburger.)

is the *zygote*. Both the ovum and the male gamete were haploid, and the consequence of their fusion is to initiate the new diploid phase, which forms the *embryo*. The process is variable in different genera of Conifers, and rather complicated.

In *Pinus* and its allies the nucleus of the zygote divides at once, first into two and then into four. The resulting nuclei sink to the base of the egg, lying in a single plane. Divisions follow to form four tiers consisting of four cells each (Fig. 255). Of these the lowest but one elongate as the suspensors (*s*); the lowest form the embryonic tier (*e*). In the Pines these may either form together a single embryo, or they may separate, each borne on its own suspensor, and so four embryos may result from one fertilisation. As there are several archegonia, and each may be fertilised, a high degree of *polyembryony* is possible. As a rule one embryo in each ovule secures the ascendency over the others, and the rest are absorbed. It has been calculated that in the Scots Pine only about one per cent. of the potential embryos are matured.

The maturing embryo, borne on the end of its elongating suspensor, is thrust downwards into the substance of the endosperm. With less regular segmentation than that in Angiosperms it matures into the germ, which in the ripe Pine-Seed is cylindrical in form. It is terminated by an apical cone, round which cotyledons, varying to

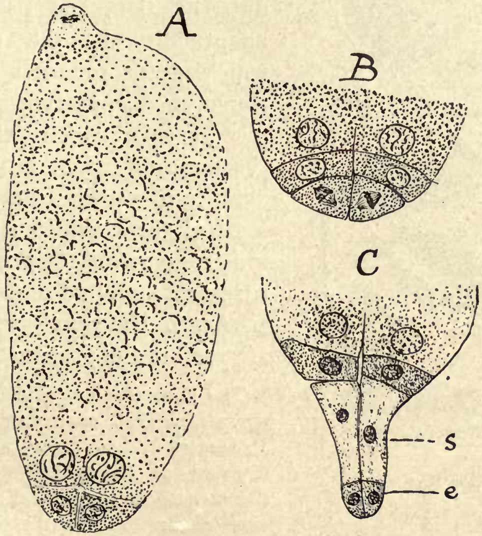


FIG. 255.

Pinus Laricio, stages of embryology. *A* shows two tiers of four cells at base of the archegonium. *B* shows three tiers, and the last division proceeding in the lowest tier. *C* shows the tier of suspensors (*s*) elongating, and carrying forward the lowest embryonic tier. (After Coulter and Chamberlain.)

the number of fifteen, are arranged in a ring. The radicle is massive, with the large root-cap characteristic of Gymnosperms. The female prothallus persists as the nutritive endosperm; the nucellus is crushed between the enlarging endosperm and the hardening seed-coat. The seed is thus albuminous, which is the case for all Gymnosperms. Its parts when mature correspond in nature and position to those of the seed in Angiosperms (Fig. 256, I.).

A period of rest is followed by germination of the seed. The embryo, drawing upon the nutritive endosperm, enlarges, and the radicle projects and grows down (Fig. 256, II.). The hypocotyl elongates, and the seed is carried above ground. The tips of the cotyledons remain within it till the store is exhausted, when it is cast off, and the cotyledons expand round the central plumule (Fig. 256, III.). Thus the seedling is established.

On comparing the two Divisions of Seed-Plants substantial similarity is seen in the leading facts of form, structure, and physiology. But there are many details which support the geological history of Gymnosperms in showing that they are relatively primitive among Seed-bearing Plants. This is seen in their lower degree of vegetative differentiation, and their less ready adaptability to the surroundings, which gives to these plants their stereotyped appearance. Their simpler vascular construction points in the same direction, in particular the absence of vessels from the wood of most of them, which is matched by some members of the primitive Angiospermic Family of the Magnoliaceae (*Drimys*). But the clearest indications are seen in the propagative details.

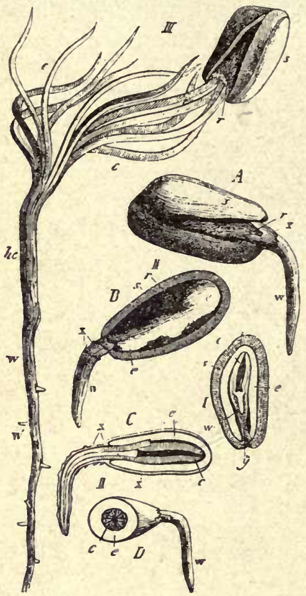


FIG. 256.

Pine seed and germination. I. Median section of seed; y=micropolar end. II. germination. III. Ditto later; s=seed-coat; e=endosperm; c=cotyledons. w=primary root; hc=hypocotyl. (After Sachs.)

The chromosome-cycle is as in Angiosperms. The sporophyte is diploid. Reduction takes place at the tetrad-division of the pollen-mother-cell and the megaspore-mother-cell, while duplication occurs at fertilisation. All the divisions which occur between reduction and fertilisation are haploid, and those cells constitute the *gametophyte.* Those in the microspore and in the pollen-tube represent the *male prothallus*; those in the megaspore or embryo-sac constitute the *female prothallus*, or *endosperm.* The most notable point for comparison with the Angiosperms is that in both cases the cell-divisions that precede fertilisation are more numerous than in Angiosperms. In the pollen-grains the first cells that are obliterated are obviously vestigial, and may be held as representing a vegetative region of the male prothallus. But such facts are in contrast to the simpler method of deposit of the grain directly upon the nucellus. The origin and position of the megaspore are as in Angiosperms. The difference again lies in the complexity of the contents. For a bulky and definitely formed tissue of the *endosperm fills it before fertilisation*, while *archegonia*, with ovum, ventral-canal-cell, and neck are present. This represents a female prothallus, with its sexual organs more definitely formed than in Angiosperms, though resembling those seen in the lower Pteridophytes. The process of fertilisation, and its method by means of a pollen-tube and non-motile gamete, are the same in the Coniferae as in Angiosperms. But in certain very primitive Gymnosperms, viz. *in the Cycads and Ginkgo, the gametes are themselves motile* (Fig. 257), and of extraordinary size. They are liberated from the pollen-tube, and have free movement before fertilisation, by means of numerous cilia, in fluid present in a chamber just above the archegonia. Thus they make their own way to the archegonial neck. This is a specially significant fact for comparison with the Pteridophyta, where the male gametes are always motile.

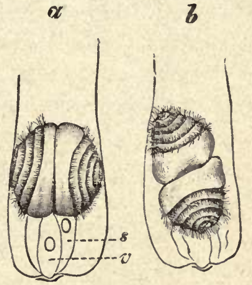


FIG. 257.
End of pollen-tube of *Zamia*, a Cycad, showing the prothallial cell (*v*), the sterile sister-cell (*s*), and the two spermatozoids. *a*, before movement of the spermatozoids has commenced. *b*, after beginning of ciliary motion. (× about 75.) (After Webber, from Strasburger.)

The general effect of comparisons between Gymnosperms and Angiosperms is to show that in the former the balance between the two generations is less uneven than in the latter. The complexity of the sporophyte is less in Gymnosperms, though its mere size may be very great. The complexity of the gametophyte, both male and female, is greater. But still the cycle of events in the alternating generations is essentially the same as in the higher Seed-bearing Plants. Such differences, slight though they may at first appear, gain in importance when seen in the light given by the study of the Pteridophyta.

DIVISION III.

PTERIDOPHYTA.

CHAPTER XX.

(*A*) LYCOPODIALES.

We now leave the Seed-Bearing Plants. The Seed which characterises them includes parts which belong to three generations. The Seed-Coat is part of the parent Sporophyte. The Endosperm, whether temporary or persistent to ripeness, represents the Gametophyte generation. The Germ is the new generation derived from it. The Seed is thus a composite structure, and being so it cannot have been of primitive origin. Its real nature, and how it was produced in the course of Descent can only be explained by comparison of Plants lower in the scale, belonging to the Division of the Pteridophytes; for it is from such seedless types that the Seed-Plants have arisen.

The Pteridophyta include the Club-Mosses (Lycopodiales), the Horse-tails (Equisetales), and the Ferns (Filicales), together with some other less familiar types of Plants, some of which are only known as Fossils. All of these are represented in the Palaeozoic Period. There is thus no doubt of the extreme antiquity of these types, which is shown by their characters as well as by their history. An important feature which they all share is that the female organ is a flask-shaped body called an *archegonium*. Such a body has already been seen in Gymnosperms, and it is also found in the Mosses (Bryophyta). In fact the archegonium is the general type of female organ for all the primitive Plants of exposed Land-Surfaces, which may accordingly be styled collectively, the *Archegoniatae*. For the present purpose of comparison with Seed-Plants a few examples selected from the Pteridophyta will suffice, of which the most important will be the genus *Selaginella* from the Lycopodiales, and some common Fern from the large series of the Filicales.

The LYCOPODIALES, to which *Selaginella* belongs, are Vascular Plants with relatively small leaves (*microphyllous*), borne upon an axis which is usually branched profusely, and rooted in the soil. The branching is by forking (*dichotomy*) both of root and stem. But there is frequent transition to *monopodial branching*, that is by outgrowth of the branch, or root, laterally below the apex of the original part. Dichotomy is prevalent also in their early fossil relatives, and is frequent among plants lower in the scale of organisation. More or less definite *cones*

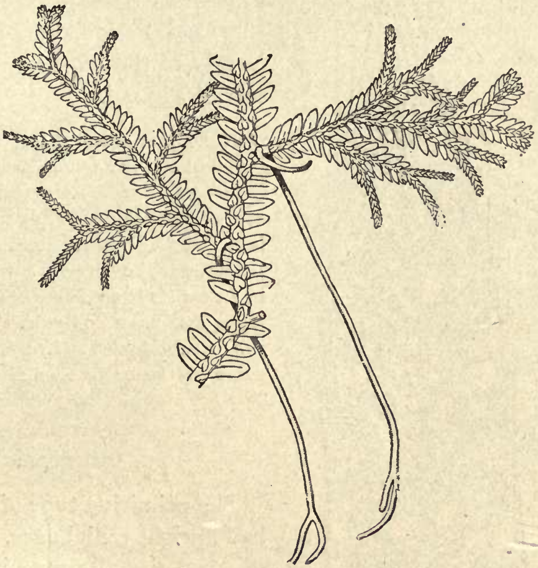


FIG. 258.
Part of the shoot of *Selaginella Martensii*, showing its "espalier" form, and minute unequal leaves. It is seen from above, and the forking rhizophores are directed downwards. (Nat. size.) (After Goebel, from Strasburger.)

or *strobili* are borne at the ends of the branches. Compressed in the axil of each leaf of the cone is a *single sporangium*, that opens when ripe like an oyster, by a marginal slit. These characters of the sporangium are common for the Lycopodiales, modern and ancient.

The Lycopodiales are represented in the British Flora by one species of *Selaginella* (*S. spinulosa*). But over 300 other species of the genus are widely spread, chiefly in the tropical zone, and many are in cultivation. They are mostly low-growing, and often shade-loving and straggling plants (Fig. 258). Another British representative is a curious inhabitant of fresh-water lochs, *Isoetes lacustris*, with its long leaves crowded upon a short succulent stock, which is fixed by dichotomous roots in the mud at the bottom. Others are the Club Mosses (*Lycopodium*), of which some five species grow on heaths and moors, chiefly in hilly districts; while nearly 100 other species are widely spread through the tropics and temperate zones. They also are low-growing plants, and some are epiphytes. These inconspicuous plants are the meagre present-day representatives of a type which grew to tree-like size in the Coal Period, and contributed largely to the organic remains preserved as Coal.

FIG. 259.
Selaginella inaequalifolia. *A*, fertile branch, half natural size. *B*, its tip in longitudinal section, with microsporangia to the left, and megasporangia to the right. (After Sachs.)

The Lycopodiales are divided into two Series, the *Ligulatae*, which include *Selaginella* and *Isoetes*, and most of the early fossil types. They are characterised by a minute scale, or ligule, borne on the upper surface of each leaf near its base (Figs. 260, 261). The *Eligulatae* have no ligule. They include the Club-Mosses (*Lycopodium*), and some of the early fossils.

SELAGINELLA.

The primitive type of *Selaginella* had upright radial axes, with leaves of equal size all round it; and this is the case in *S. spinulosa*. But most of the species have a much-branched, dorsiventral shoot of an "espalier" type, sometimes simulating highly compound leaves (Fig. 258). On these shoots the actual leaves are disposed in four longitudinal rows, those on the lower flanks being larger, those on the upper smaller. Such shoots are commonly propped up by root-like organs (*rhizophores*), borne at the forkings of the shoot, and themselves showing very regular dichotomy. They are not actually roots, but on reaching the ground they give rise to roots endogenously: hence their name. Structurally *Selaginella* is relatively simple. The vascular system is essentially of the same type as that to be described below for Ferns. It consists of sharply circumscribed stelar tracts, with tracheides but no vessels, and no secondary thickening.

But the greatest interest lies not in the structure of the plant so much as in its *sporangia*, and the germination of its spores: for these give lines of comparison with the Seed-Plants. The strobilus or cone that bears them is distal on a vegetative branch, and even in the flattened species it has the primitive radial form, all the sporophylls being of equal size (Fig. 259, *A*). A longitudinal section shows that a short-stalked sporangium is borne in the axil of each. These sporangia

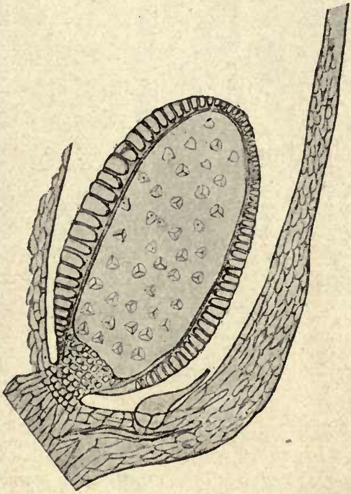


FIG. 260.

Microsporangium of *Selaginella apus*, in median vertical section, containing numerous microspores. The ligule is seen in Figs. 260, 261, as a small tongue-like body, at the base of the leaf. (× 55.) (After Miss Lyon.)

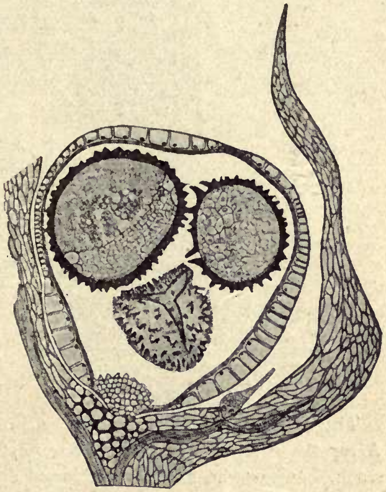


FIG. 261.

Megasporangium of *Selaginella apus*, in median vertical section, showing three of the four megaspores. (× 21.) (After Miss Lyon.)

are of two sorts, which are associated in the same strobilus, but disposed in various ways in different species. In *S. inaequalifolia* those on the right side of the section shown in Fig. 259, *B*, are all megasporangia, with four large spores in each; those on the left-hand side are microsporangia, containing many small microspores. In form the sporangia are alike; they differ in the number and size of their contents. A mature microsporangium, with its subtending sporophyll and ligule, is shown in median section in Fig. 260. The line of dehiscence is distal, where the cells of the wall are smallest, and the structure of the cells of the wall is such as to lead to its valves being everted as they dry on ripening, so that the spores are shed. The mature megasporangium behaves in a similar way, but the spores are ejected forcibly by pressure of the everted valves upon them (Fig. 261). The spores fall upon the soil, and germinate there. *Thus both the megaspores and microspores are shed from the parent plant.*

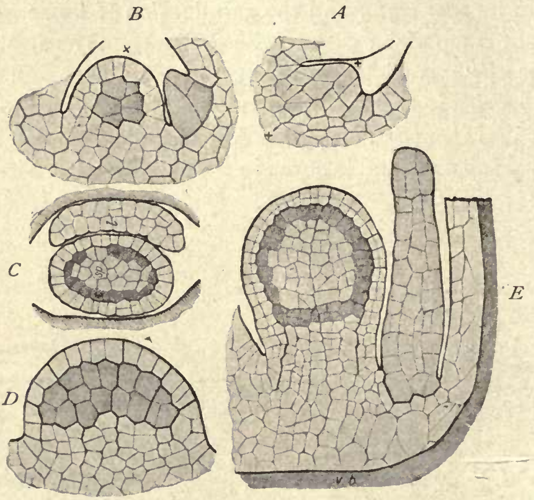


FIG. 262.

A, *B*=radial sections through young sporangia. *C*=transverse section of one more advanced. *D*=tangential section. *E*=radial section of an older sporangium, with ligule: the tapetum is shaded, and the sporogenous cells lie within. (*A*, *B*, *C*, *D*=350; *E*=200.) F. O. B.

The sporangium arises in the axil of the sporophyll, just within the ligule. After the first segmentations are past it is found to consist of a short thick stalk, bearing the slightly flattened sporangial head. This contains a group of sporogenous cells, from which later a surrounding tapetal layer is cut off. Outside this is a wall composed of two layers of cells (Fig. 262, *E*). Later the spore-mother-cells round themselves off, becoming isolated in a fluid that fills the enlarging cavity. *Up to this point it is impossible to tell which type of spore the sporangium will produce.* This fact indicates that the megasporangium and microsporangium are differentiated from one original type. In the case of a microsporangium all the spore-mother-cells undergo the tetrad division, and a large number of microspores is the result. But if it is to be a megasporangium, only one (in some species two) of the spore-mother-cells develops further (Fig. 263), the rest becoming disorganised. The four megaspores, with rugged walls, occupy the whole sporangium at maturity (Fig. 261).

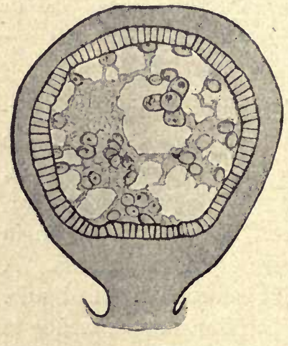


FIG. 263.

Selaginella spinulosa. Section of megasporangium, showing the single fertile tetrad still very small, and the rest of the sporogenous cells arrested. (×100.) F. O. B.

The germination of both types of spores may begin before they are shed, but it is continued on the moist soil. The *microspore* first partitions off a lenticular cell, which is vestigial like those in the pollen-grains of *Pinus*, representing a *male prothallus*. The rest of the contents segment to form a wall of eight sterile cells surrounding a numerous group of *spermatocytes* (Fig. 264, *A*). A mucilaginous change appears in the walls of these latter cells. Meanwhile their protoplasts form each a single curved *spermatozoid*, motile in water by two cilia. Swelling of the mucilage by water bursts the wall of the spore, and the spermatozoids escape (Fig. 264, *B*).

The germination of the *megaspores* produces an internal tissue of greater extent, which may be styled the *female prothallus*. Its develop-

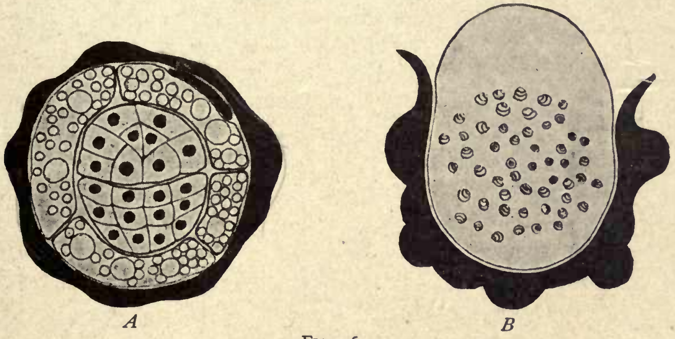


FIG. 264.
A, microspore of *S. apus* after germination. *B*, the same just before extrusion of spermatozoids. (After Miss Lyon.)

ment begins below the meeting of the three converging ridges of the tetrahedral spore, and it extends into the spore-cavity, which is stored with nutritive material (Fig. 261). The increase in bulk of the contents ruptures the wall of the spore along the converging ridges, so that the surface of the tissue is exposed (Fig. 265, I.). Near the central point the first archegonium appears, while laterally others may be formed later, but not in regular succession. A vertical section through a megaspore of *S. denticulata* shows it completely filled with tissue of the prothallus, while its exposed surface bears rhizoids (*rh*) and archegonia in various stages of development (*ar*) (IV.). The archegonium consists of a neck (*n*) composed of two tiers of four cells each: a canal-cell (*c.c.*), ventral-canal-cell (*v.c.c.*), and the ovum (*ov.*); all of which were derived by segmentation from a single superficial cell of the prothallus (V.). When mature the neck is open, the canal-cell and ventral-canal-cell have disappeared, and the *ovum*, which is now a rounded primordial cell, is open to access of the spermatozoids. As both types of spore germinate together, *fertilisation* is readily carried out.

After fertilisation the *zygote* secretes a protective wall, and elongating in the axis of the archegonium, segments repeatedly (VI.-VIII.) to form a suspensor (*s*) which, as in the Gymnosperms, thrusts the embryo down deep into the prothallus (IV.). The distal cell soon enlarges, and divides. It gives rise centrally to the apex of the stem (*st*), with

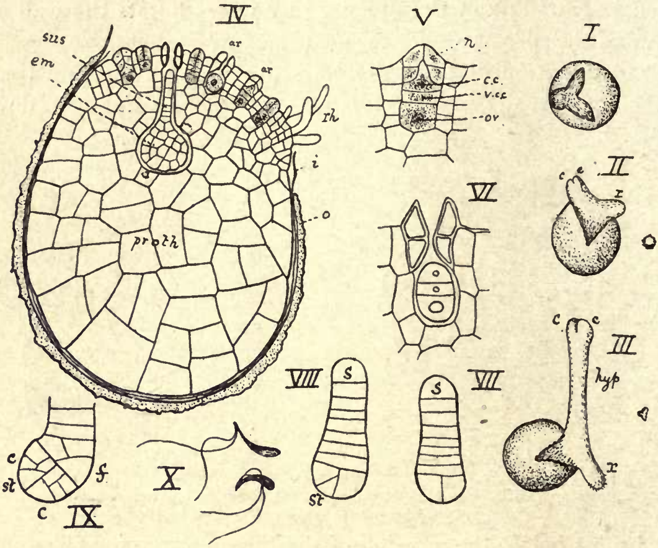


Fig. 265.

Embryology of *Selaginella denticulata*, after Bruchmann. I.-III. (× 12½) show germination of megaspore. IV. vertical section of megaspore showing prothallus, archegonia, and embryo (*em*) with suspensor (*sus*) (× 50). V.=a mature archegonium. VI.-IX.=stages of developing embryo. X.=spermatozoids of *S. cuspidata*, after Belajeff. (× 250.)

cotyledons right and left (*c*, *c*). Meanwhile unequal growth turns it to one side, and the convex side enlarges into the suctorial "foot" (IX. *f*). Lastly, the first root (*wt*) is initiated by periclinal divisions close to the attachment of the suspensor, and on the same side of the embryo (Fig. 265 *bis*, *A*, *B*). All the parts of the young embryo have thus been produced, while the apex of the axis occupies the distal position from the very first in the curved embryo. As the axis and root grow they protrude from the ruptured spore, the root turning downwards, and the elongating hypocotyl turning upwards (Fig. 265, II. III.). The cotyledons already bear ligules (*l*, Fig. 265 *bis*). The further development is merely a matter of continued growth and branching.

It will be noted that there is no interruption of the development by a period of rest, as in the matured seeds of Flowering Plants.

The life-cycle of *Selaginella*, though it does not involve the formation of a seed, or include any dormant period, corresponds in its essentials to that in Flowering Plants. In both cases the plant itself is the diploid, or sporophyte generation. The events may be compared, starting from the production of the spore. The fact that the pollen-sac and ovule of seed-bearing plants differ in form and position from the microsporangia and megasporangia of *Selaginella* does not prevent their comparison respectively with them. In the pollen-sac, as in the microsporangium of *Selaginella*, a tetrad-division leads to the

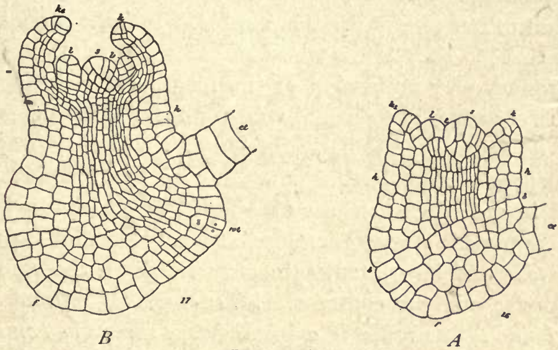


FIG. 265 *bis*.

Embryos of *Selaginella denticulata*, after Bruchmann. *et* = suspensor. *wt* = root. *f* = foot. *bb* = basal wall. *h* = hypocotyl. *s* = apex. *k*, k_1 = cotyledons. *l* = ligule. (After Bruchmann.)

formation of four spores from each tetrad. The microspores in each case are shed on rupture of the sporangial wall. In the ovule, as in the megasporangium of *Selaginella* a tetrad-division leads up to the formation of the megaspore. In both cases only one spore-mother-cell as a rule undergoes the division, but in both cases there may occasionally be more than one. In Seed-Plants usually only one megaspore, or embryo-sac, is matured. In *Selaginella* commonly four, and occasionally more ; but sometimes two, or even only one. Thus in point of origin, in manner of production and sometimes in number, the megaspore corresponds to the embryo-sac. *The difference lies in the fact that in* SELAGINELLA *the megaspore, with its thick protective wall, is shed on rupture of the megasporangium ; in Seed-Plants the megaspore, or embryo-sac, is retained within the nucellus.* The embedded sac is thus able to obtain continued nourishment. The biological advantage thus gained offers a ready explanation of the universal adoption of this derivative state by Seed-bearing Plants.

The germination of the microspore of *Selaginella* compares with the maturing of the pollen-grains of Gymnosperms in the formation first of the prothallial cell, which corresponds to the cells which are obliterated in them. The further development in *Selaginella* is more elaborate, for there is a protective layer of cells of the wall, and a considerable mass of spermatocytes, each giving rise to a spermatozoid. In *Pinus* the gametes are non-motile, and only two in number. But it has been noted in *Cycas* and *Ginkgo* that they are motile, and in *Microcycas* they are numerous. Such instances show that the products of development within the microspores of Gymnosperms and of *Selaginella* are comparable. In both cases they act as male gametes.

The product of germination of the megaspore in *Selaginella* is a prothallus, bearing archegonia which on fertilisation produce an embryo, or several. Similarly, in *Pinus* the embryo-sac develops the endosperm before fertilisation. It also bears archegonia corresponding in essentials to those of *Selaginella*, which on fertilisation produce embryos. It may therefore be concluded that the megaspore of *Selaginella* and its contents are comparable to the embryo-sac of Gymnosperms, and its contents. *When parts of different organisms are thus found to be similar in origin they are said to be homologous one with another.* We conclude from their development that the microspore of *Selaginella* is homologous with the pollen-grain of *Pinus*, and of Seed-Plants at large; and that the megaspore of *Selaginella* is homologous with the embryo-sac of *Pinus*, and of Seed-Plants at large. And this holds notwithstanding that in *Selaginella* both megaspores and microspores are shed from the parent plant, but in Seed-Plants only the microspores are shed, while the megaspore is retained.

If further evidence were required of the correctness of these conclusions, it is found in the fact that in certain fossils belonging to the Lycopodiales (*Miadesmia* and *Lepidocarpon*) a seed-like structure did actually exist. It resulted from the retention of the megaspore in the sporangium, just as it is seen as a permanent and constant feature in Seed-Plants. The conclusion is that *Selaginella* stands in this respect on a more primitive footing than these fossils, or than the whole of the successful Series of Seed-bearing Plants.

It has been seen that in *Selaginella* the megasporangia and microsporangia are alike in their origin, and development up to the stage of the spore-mother-cells. It follows that these sporangia also are homologous one with another, and the spores that they produce homologous also. It is only a step further to a condition where the sporangia and spores are all alike, in structure and in size, up to full maturity. This state is actually seen in *Lycopodium*, in most Ferns, and in all Mosses, which are accordingly styled *homosporous*. The condition with the spores differing in size is called *heterosporous*. From the evolutionary point of view the latter is the later and derivative state, and it has been adopted exclusively by all the higher Land-growing Plants. The homosporous is the more primitive state, and it will now be illustrated in the Ferns and Mosses; plants which in this, as well as in other respects, stand lower in the scale of Evolution.

CHAPTER XXI.

(*B*) FILICALES.

The living Ferns include more than 7000 species, widely spread over the earth's surface from the Equator to the Arctic Regions. Some 39 of these are British. Though a few live actually in water, others are distinctly Xerophytic, and able to resist extremes of drought. But the vast majority live in moist and often in shaded positions, and, as will be seen later, external fluid water is necessary for the completion of the normal cycle of their life. The Fern Plant is with very few exceptions perennial. It consists of a shoot which may or may not be branched, and is attached to the soil by numerous fibrous roots. The shoot consists of axis and leaves, as in the Flowering Plants, but usually without axillary buds. The leaves are large in proportion to the stem that bears them. Often they are highly branched, with two rows of lateral pinnae that are branched again repeatedly. This, together with their delicate texture, gives the feathery appearance to the leaves of most Ferns (Fig. 266). It is specially conspicuous in the large Tree-Ferns, where each leaf may be many feet in length. This habit (megaphyllous) contrasts strongly with that of the Lycopods with their small unbranched leaves (microphyllous).

The Coal Period has been sometimes described as "The Age of Ferns." It is true that large-leaved Fern-like Plants were frequent then. But many of these have been lately shown to have been Seed-bearing Plants (Pteridosperms), whereas Ferns have no seeds. The question has then been raised whether Ferns existed at all at that early time. There are at least three types which can only have been Ferns that did live then, and some similar to them survive to the present day. But many of the Ferns we know are relatively modern. It is doubtful whether at any time a more varied Fern-Flora has existed on the earth than at the present day. If that be so, the present is as much the age of Ferns as any that has gone before.

The Ferns show a comparatively primitive cycle of life. It consists of two alternating and physiologically independent phases, or generations, the one diploid (non-sexual), which is the *sporophyte*, the other haploid (sexual), which is the *gametophyte*. The former is what is

FIG. 266.
Nephrodium Filix-mas, Rich. Fertile leaf about one-sixth natural size, the lower part with the under surface exposed. To the left a single fertile segment, bearing kidney-shaped sori, enlarged about seven times. (After Luerssen.)

known commonly as the *Fern-Plant;* the latter is a small green scale-like body, which is called the *Prothallus*. Naturally, as the former is the better-known phase, it will be described first.

MALE FERN AND BRACKEN

The large-leaved shoot of the Fern Plant may grow upright, and usually unbranched, as in Tree-Ferns, and the Royal Fern (*Osmunda*);

or obliquely, as in the common Male Fern (*Nephrodium*) (Fig. 267); or horizontally with a creeping habit, as in the Bracken (*Pteridium*), or the Common Polypody. When upright the internodes are short, and the numerous leaves take the basket-like grouping, as in the

FIG. 267.

Nephrodium Filix-mas, Rich. *A*, stock in longitudinal section. *v*=the apex. *st*=the stem. *b*=the leaf-stalks. *b′*=one of the still folded leaves. *g*=vascular strands. *B*=a leaf-stalk, bearing at *k* a bud with root at *w*, and several leaves. *C* is a similar leaf-stalk cut longitudinally. *D*=a stock, from which the leaves have been cut away to their bases, leaving only those of the terminal bud. The spaces between the leaves are filled with numerous roots, *w*, *w′*. *E*, stock from which the rind has been removed to show the vascular network, *g*. *F*=a mesh of the network enlarged, showing the strands which pass out into the leaves. (After Sachs.)

Male Fern; when creeping the internodes are longer, so that the leaves are isolated, as on the underground rhizome of the Bracken, the leaves being here the only part above ground. The stems of Ferns have unlimited apical growth, and sometimes fork at their ends, as the Lycopods do. But buds may also appear at the leaf-bases, a condition seen in the old leaves of the Male Fern (Fig. 267, *B*). A general peculiarity of Ferns is the crozier-like curvature of their young leaves, the adaxial face growing at first more slowly. But later it catches up the abaxial face, so that the leaf flattens out as it matures. This habit is effective in protecting the curled tip of the leaf, since in Ferns apical growth is long continued, and the tissues are delicate. The stem and leaves, especially while young, are often densely covered either with

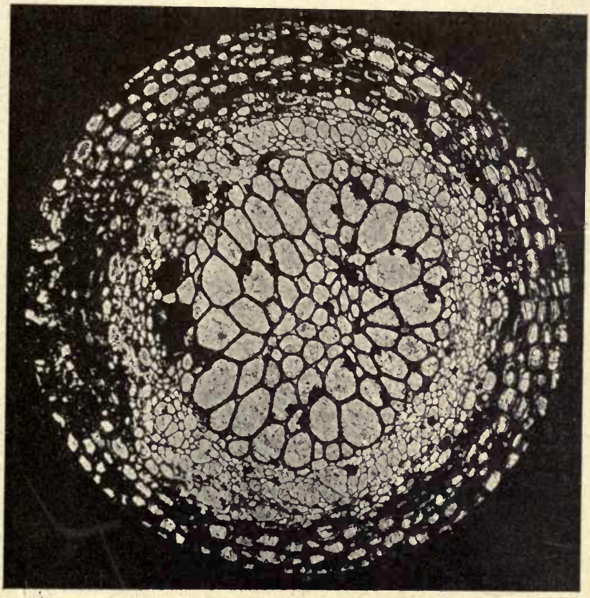


FIG. 268.

Transverse section of a fossil-Fern, *Botryopteris cylindrica*, showing a protostele with solid central core of xylem, and peripheral phloem. This is a fossil from the Palaeozoic, and it illustrates how perfect the preservation of structure may sometimes be in fossils of very early periods.

hairs (*Osmunda*), or chaffy scales (*Nephrodium*), which protect the young parts against drought, but are liable to fall away later.

In their general construction Ferns resemble Flowering Plants. They have a superficial *epidermis*, and a conducting system of *vascular tissue* embedded in *ground-tissue* which is parenchymatous, but often it also encloses strands or islands of hard brown *sclerenchyma*, while hard stony or horny sheaths frequently form the surface of stem and leaf-stalk. The epidermis and ground tissue call for no detailed description. The chief interest lies in the vascular system. In ancient fossil Ferns, such as *Botryopteris*, in many primitive living

Ferns, and generally in young sporelings there is a simple *stele* of a type called a "protostele," having a solid xylem-core, and phloem surrounding it. This is believed to have been the primitive structure for them all. It is well shown in *Botryopteris* (Fig. 268). Occasionally this state may be retained through life (*Hymenophyllum*, *Lygodium*). But in the vast majority of Ferns the stele expands as the plant grows stronger, and the leaves larger; and in various ways it becomes segregated into a number of vascular strands (*meristeles*), arranged in a cylindrical network (Fig. 267 *E*, *F*). Each mesh in *Nephrodium*

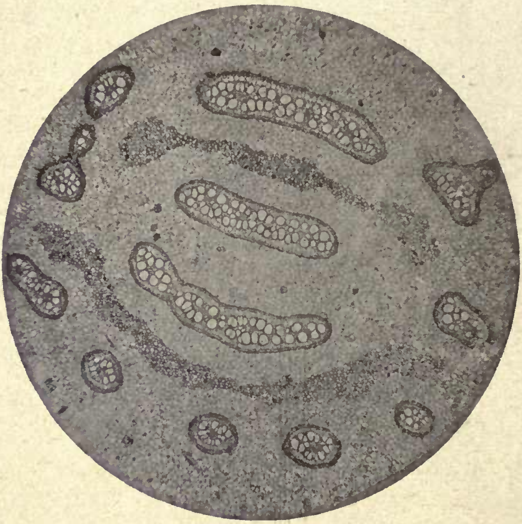


FIG. 269.
Transverse section of rhizome of Bracken, omitting the external band of sclerenchyma, and showing the outer and inner series of meristeles, and the irregular bands of dark sclerenchyma between them. (×10.)

corresponds to the insertion of a leaf-base, and is called a *foliar mesh, or gap*. The vascular strands that run out into the leaf, called collectively the *leaf-trace*, arise from the margin of it, and the cortex and pith are in direct communication through the follar gaps. *Nephrodium* gives a comparatively simple examplc of this subdivision of the stele, which is characteristic of most Ferns, and is to be regarded as derived from the primitively undivided protostele. The leaf-trace in different kinds of Ferns may be a single strand, or many. In either case it sends out branches into the pinnae and pinnules, and they end either in an open venation, as in *Nephrodium* or *Pteridium* (Fig. 266); or in a network of veins, as in the Adder's tongue. Thus the vascular arrangement in the leaves of Ferns resembles that in Flowering Plants more nearly than does that of their stems.

For the study of the tissues composing a vascular strand, a rhizome with long internodes, such as the Bracken, gives the best results. In a transverse section taken between the leaf-insertions an outer and inner series of vascular strands is found, separated by an incomplete ring of sclerenchyma. The outer series corresponds to the mesh-work of *Nephrodium*, the inner are accessory, or medullary meristeles

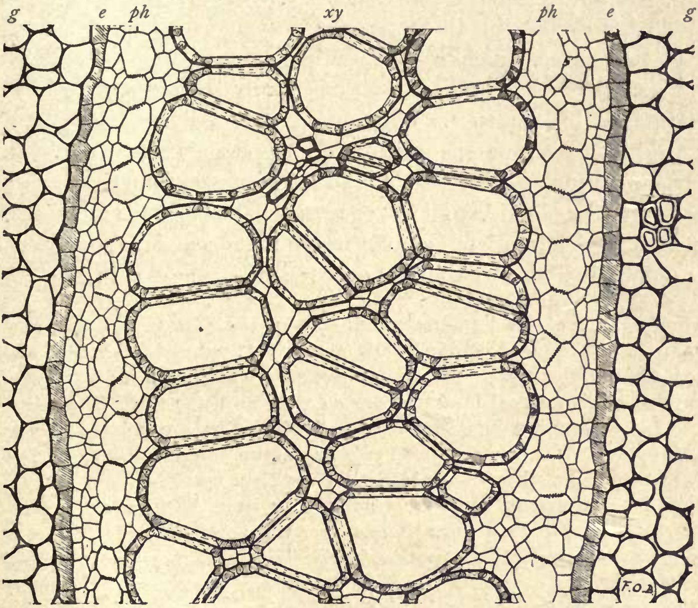


FIG. 270.
Part of a transverse section of a meristele of Bracken. *g*=ground parenchyma. *e*=endodermis. *ph*=phloem with sieve-tubes. *xy*=xylem, with large scalariform tracheides. Some smaller tracheides lying centrally are the proto-xylem. (×75.)

(Fig. 269). Each one is circumscribed by a complete endodermis. This is usual in Ferns. Each consists of a central core of xylem, surrounded by phloem; in fact they repeat the main structure of the protostele itself. A small part of one of them, examined under a high power, gives the following succession of tissues (Fig. 270). Passing inwards from the starchy ground-tissue, with intercellular spaces (*g*), the layer of brownish cells of the *endodermis* (*c*) forms a continuous barrier, delimiting the strand sharply. Within it follows the *pericycle*, with its cells not very regularly disposed, but corresponding roughly to the cells of the endodermis, both having been derived by division from a single layer. Within this comes the *phloem* (*ph*), with large *sieve-tubes* as the characteristic elements. They are thin-walled, with watery contents. The lateral walls where two adjoin bear the sieve-plates, and are recognised by glistening globules that adhere to them. They are embedded in parenchyma, which extends inwards into the xylem, and may be called collectively *conjunctive parenchyma*. The chief features of the *xylem* (*xy*) are the *tracheids*, which are relatively large, with a very characteristic polygonal outline. They have woody walls, and no protoplasmic contents. Where two adjoin the walls are flattened, and of double thickness, showing that each has its own share of the thickening, which overarches the pit-membrane as in the pits of Conifers. The structure is in fact essentially the same, only in Ferns the pits are liable to be extended transversely. But where the tracheid abuts on parenchyma-cells the pits are narrower. Internally, and usually about the foci of the elliptical meristele smaller tracheides are found. These are the first-formed tracheides, or *protoxylem*. The meristele of a Fern is thus concentric in construction; it is strictly delimited, and has no provision for increase in size.

The *tracheide* of the Fern resembles that of the Pine in being of spindle-form, with its thickened lignified walls marked by bordered pits. But whereas the pits in the Pine are circular, those in the Fern are liable to be transversely elongated, as is natural in tracheides so wide as these are. Their features are well seen in longitudinal sections, but better if they are isolated by maceration (Fig. 271, *A*). The elongated pits lie parallel to one another, and this is specially well seen where two wide tracheides have faced one another. From the ladder-like appearance that results they have been called *scalariform tracheides*. Examined under a high power the double outline of the pits is seen, and when the pits are small and circular the similarity to those of the Pine is plain (Fig. 271, *B*). In most Ferns the pit-membranes persist, but in *Pteridium* they appear to be liable to be broken down, and the cavities thrown together technically as in vessels. The tracheides of the protoxylem are seen in longitudinal section to be spiral or reticulate, as in other Vascular Plants.

The *sieve-tubes* are also spindle-shaped, and are without companion-cells. Their cellulose walls are swollen. Where two sieve-tubes adjoin, numerous thinner sieve-areas of irregular outline are borne. They are found to be perforated by very fine protoplasmic threads extending between highly refractive globules that adhere to the walls (Fig. 272). Such tracheides and sieve-tubes are characteristic of Ferns, and with differences of detail, of other Pteridophytes as well.

The anatomy of the *leaf* in Ferns resembles that of Seed-Plants down even to the collateral structure of the vascular strands. Being chiefly shade-loving plants chlorophyll is usually present in the cells of their epidermis, and the differentiation of the mesophyll into palisade and spongy parenchyma is not marked. In these respects they resemble the leaves of Angiosperms of similar habit. In the *roots* of Ferns, as in those of Seed-Plants, there is a superficial piliferous layer, a broad cortex, and a contracted stele. But usually the inner cortex is very strongly lignified, up to the endodermis, which is thin-walled (Fig. 273). The pericycle which follows is variable, sometimes being greatly enlarged as a water-storage-tissue. The protoxylems are peripheral, and two or sometimes more in number, the phloem-groups alternating with them. In fact the root of a Fern is constructed essentially on the plan of that in Seed-Plants. As there is no secondary thickening the roots of

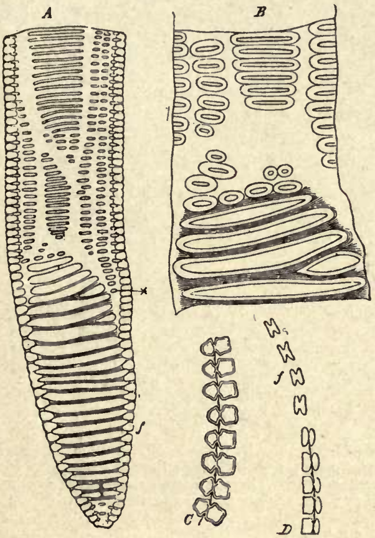


FIG. 271.

Tracheides of *Pteridium*. *A* = the end and about one-third of the length of a tracheide, with part of the lateral wall in surface view, showing scalariform marking (× 100). *B* = part of *A* magnified 200. *C* = thin longitudinal section through a lateral wall where two tracheides adjoined (× 375). *D* = similar section through oblique wall at *f* (× 200). There the pit membranes are not visible. (After De Bary.)

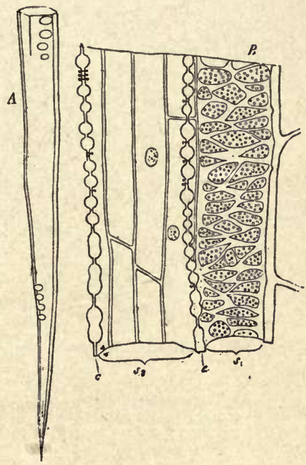


FIG. 272.

Sieve-tubes of *Pteridium*. *A* = end of a tube separated by maceration (× 100). *B* = longitudinal section through phloem showing one sieve-tube with the sieve-plates (s_1) in surface view. *c*, *c* are walls shown in section, bearing sieve-pits (× 200).

Ferns are all fibrous. The lateral roots arise opposite to the protoxylems, and there they originate from definite cells of the endodermis, which may often be recognised beforehand by their size and contents.

While we recognise the substantial similarity of Ferns and Seed-Plants in respect of form and structure of stem, leaf, and root, these plants differ in the construction of their *apical meristems*. In Seed-Plants these are small-celled tissues, and more or less definitely stratified (pp. 17, 77). In Ferns such as *Osmunda*, *Nephrodium* or *Polypodium*, a single large cell, the *apical or initial cell*, occupies the tip of each growing part. It has a definite shape, and segments are cut off from its sides in definite succession. As the whole tissue of the stem, leaf, or root is derived from such segments, the whole of each part is referable in origin to its apical cell, which maintains its identity throughout. The form of the cell in roots, in most stems, and in some leaves (*Osmunda*) is that of a three-sided pyramid; but where the organ is flattened, as in some stems

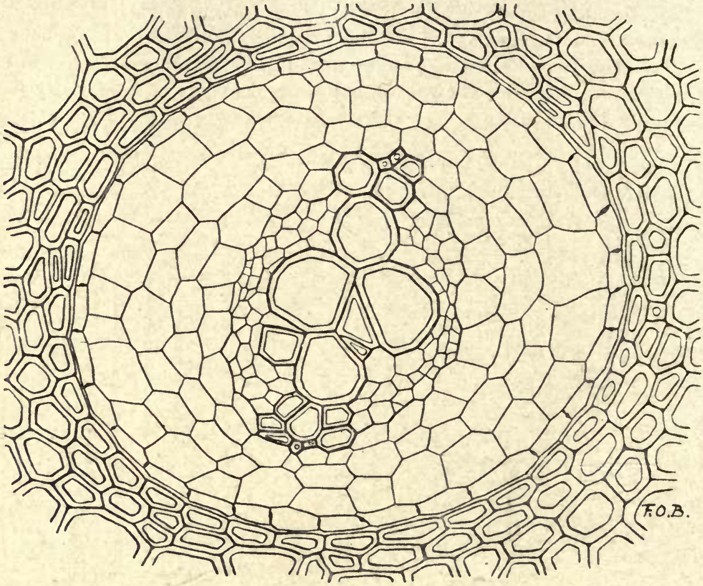


FIG. 273.
Transverse section of a root of a Fern (*Pellæa*) (× 150). Outside lies the sclerotic cortex, limited internally by a definite endodermis. There are two groups of protoxylem; a very broad pericycle, of 3 or 4 layers, surrounds the vascular tissues.

(*Pteridium*), and almost all leaves, it has two convex sides, and is shaped like half of a biconvex lens. In the former case the segments are cut off in regular succession from the three sides (Fig. 274, 276), in the latter alternately from the two sides (Fig. 275). The further subdivision of the segments to form the tissues is represented in surface view for the case of *Osmunda* in Fig. 274: and Fig. 275 shows, in the surface view of a young leaf of *Ceratopteris* how the whole member may be built up from such segments. In roots the segmentation is complicated by the origin of the root-cap. This is provided by a segment cut off from the frontal face of the pyramid, after each cycle of three has been cut off from its

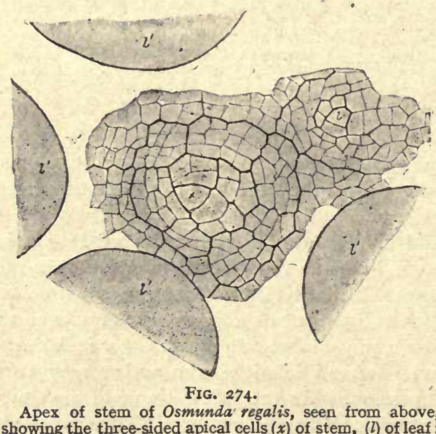


FIG. 274.
Apex of stem of *Osmunda regalis*, seen from above, showing the three-sided apical cells (*x*) of stem, (*l*) of leaf; *l′ l′*, older leaves. The successive segments of the apical cell form the whole of the apical cone. (× 83.) F. O. B.

sides (Fig. 276). Thus every fourth segment goes to form the protective cap, and renews it from within. Not only does the leaf also show continued growth and apical segmentation from its two-sided apical cell, but the lateral wings or flaps originate by the activity of rows of marginal cells. There is also a definite segmentation seen in the origin of the sporangia. Thus Ferns have not stratified meristems like Seed-Plants. The tissues of all their parts originate from segmentation of superficial cells. This is a general character of the Pteridophyta, though the details of their segmentation and the number of the initial cells are open to variation.

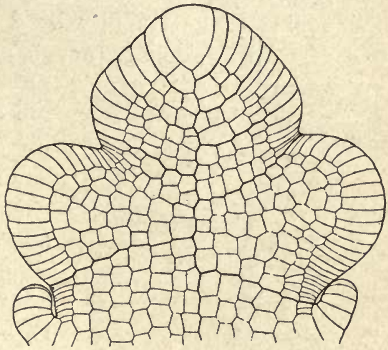


FIG. 275.

Young leaf of *Ceratopteris*, in surface view, after Kuy; showing two-sided apical cell; and the marginal series, continuous round the young pinnae. The latter do not correspond to the segments from the apical cell.

Thus constituted the Fern-Plant carries out its life on Land in essentially the same way as Seed-Plants. The structural differences are those of detail, the most important being the absence of secondary thickening in the stem. These plants have no automatic provision for increasing mechanical strength with size. In Tree-Ferns this deficiency is made up for partly by masses of hard brown sclerenchyma, which accompany and enclose the flattened

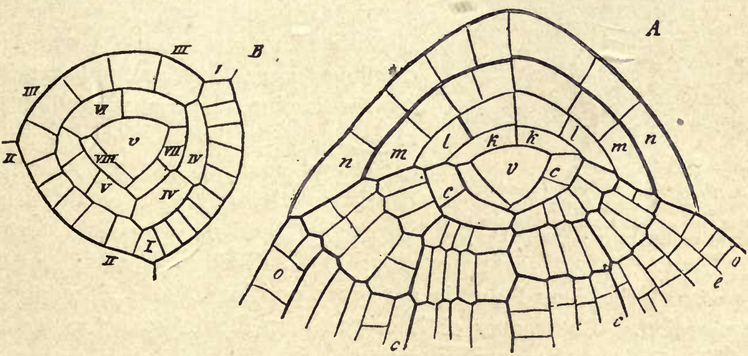


FIG. 276.

(× 250). *A* = longitudinal section through apex of the root of *Pteris*. *B* = transverse section through the apical cell of the root and neighbouring segments of *Athyrium*. (After Naegeli and Leitgeb.) *v* = apical cell. *k, l, m, n* = successive layers of root-cap. *o* = dermatogen. *c* = limit of stele. (From Sachs.)

meristeles; and their margins are usually curved outwards, thus securing increased mechanical resistance on the same principle as in corrugated columns. Their strength is further increased according to size and age by the development of masses of sclerotic, adventitious roots, matted together to form a thick investment to the original trunk, and adding to its stability by a method comparable mechanically to a cambial thickening, though quite different in origin. But such mechanical provision for increase in size are only partially effective. There is no evidence that Ferns ever ranked among the largest of living Plants.

FIG. 277.
A pinnae of a Fern (*Woodwardia*) showing many sporophytic buds on the upper surface. They correspond in position to sori on the lower surface, which are abortive.

Many Ferns increase in number by *vegetative propagation*. This may follow simply on continued growth and branching, as in *Pteridium*, where the rhizome forks frequently. Whenever progressive rotting extends from the base beyond a branching, the two apices grow on as independent plants. In this way the Bracken multiplies habitually. In *Nephrodium* buds are formed near the bases of the leaves in old plants. Again, as rotting proceeds from the base, these buds become isolated, and root themselves as new individuals (Fig. 267, *B*, *C*). In other Ferns, as in the various species of *Asplenium* so commonly grown in dwelling rooms, buds or bulbuls arise on the lamina. Being very lightly attached to the leaf they are readily shed, and root themselves independently in the soil. In some cases vegetative buds may replace the sori (Fig. 277). Such vegetative propagation of the Fern-Plant is a mere repetition of the Sporophyte generation. But sooner or later the Fern-Plant bears the *spores*, which start the alternate generation.

The *spores* are produced on certain leaves of the mature plant which are therefore called *sporophylls*, to distinguish them from those which are only nutritive. In *Nephrodium* nutritive leaves and sporophylls are alike in outline. The young plant only produces the former. But the leaves of older plants bear on their lower surface, and chiefly in the apical region, numerous groups of organs which are green or brown according to age. These are called *sori*, and consist of *sporangia* with certain protective structures. The sori vary greatly in size and form in different Ferns, which are classified according to their characters. In *Nephrodium*, as the name implies, they are kidney-shaped, as is seen in Fig. 266. Each sorus is seated on a vein, which provides its necessary nourishment. It is protected by a

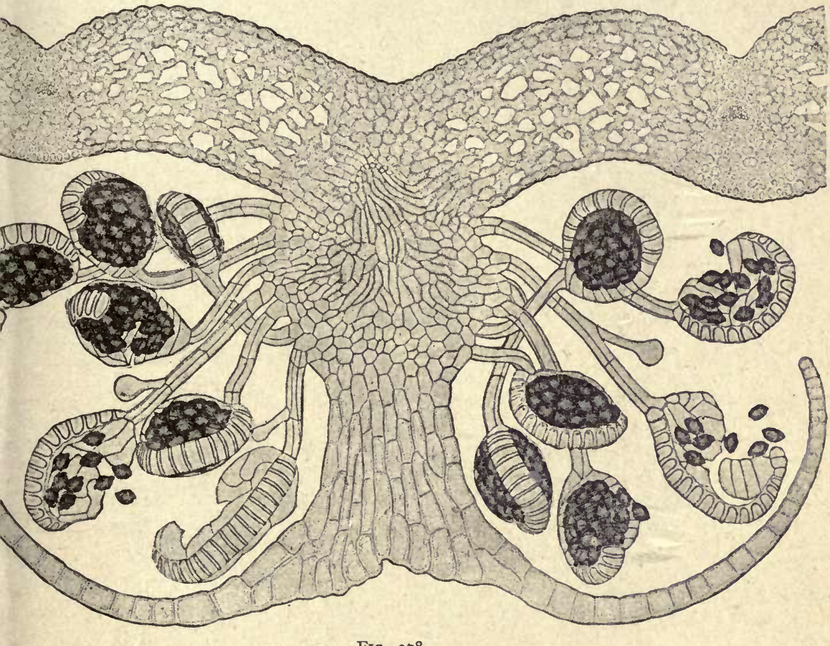


FIG. 278.
Vertical section through the sorus of *Nephrodium Filix-mas*. (After Kny.)
The adaxial surface is uppermost.

covering called the indusium, of kidney-like outline, beneath which are numerous sporangia. If a leaf bearing mature sori be laid on a sheet of paper to dry, with its lower surface downwards, the indusia shrivel, and the bursting sporangia shed the spores in such numbers that they give a clear print of the outline of the sporophyll upon the paper. The spores are dark-coloured, very minute, and are produced in millions.

A vertical section through the sorus of *Nephrodium* shows an enlarged receptacle, traversed by the vascular strand. The indusium rising from it overarches the numerous sporangia which are attached to it by long thin stalks (Fig. 278). The head of each sporangium is shaped like a biconvex lens; its margin is almost completely surrounded by a series of indurated cells, which form the mechanically effective *annulus*. This stops short on one side, where several thin-walled cells define the *stomium*, or point where dehiscence will take

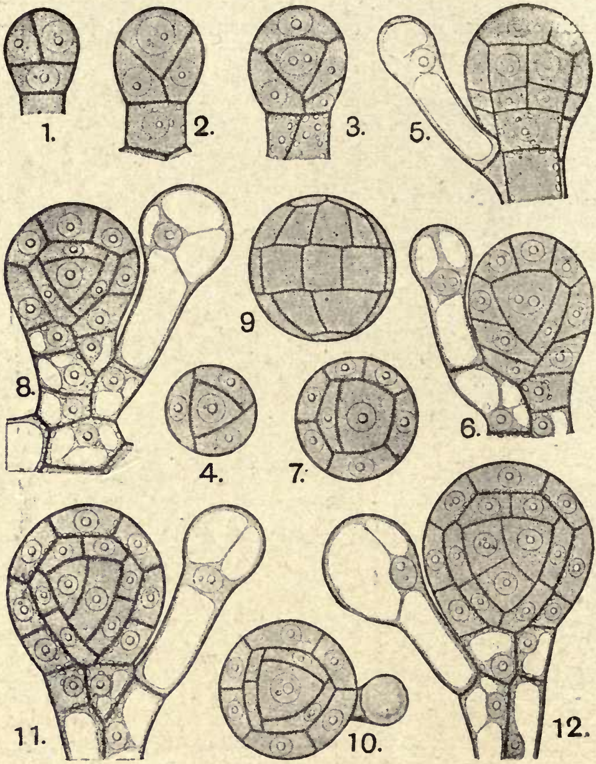


FIG. 279.
Successive young stages in the segmentation of the sporangium of *Nephrodium Filix-mas*. (After Kny.)

place (Figs. 278, 280, 4*a*, 281). Within are the dark-coloured *spores*, which on opening a single sporangium carefully in a drop of glycerine may be counted to the number of 48. Normally the sporangia open in dry air, and the dry and dusty spores are forcibly thrown out.

The origin of a sporangium is by outgrowth of a single superficial cell of the receptacle, which undergoes successive segmentations as illustrated in Fig. 279, 1-3. A tetrahedral internal cell is thus completely segmented off from a single layer of superficial cells constituting the wall. The former undergoes further segmentation to form a second layer of transitory nutritive cells called the *tapetum* (Fig. 279, 6-12), subsequently doubled by tangential fission (Fig 280, 1). The tetrahedral cell which still remains in the centre, having grown meanwhile, undergoes successive divisions till twelve *spore-mother-cells* are formed (Fig. 280, 2-7). These become spherical, and are suspended in a fluid which, together with the now disorganised tapetum, fills the enlarged cavity of the

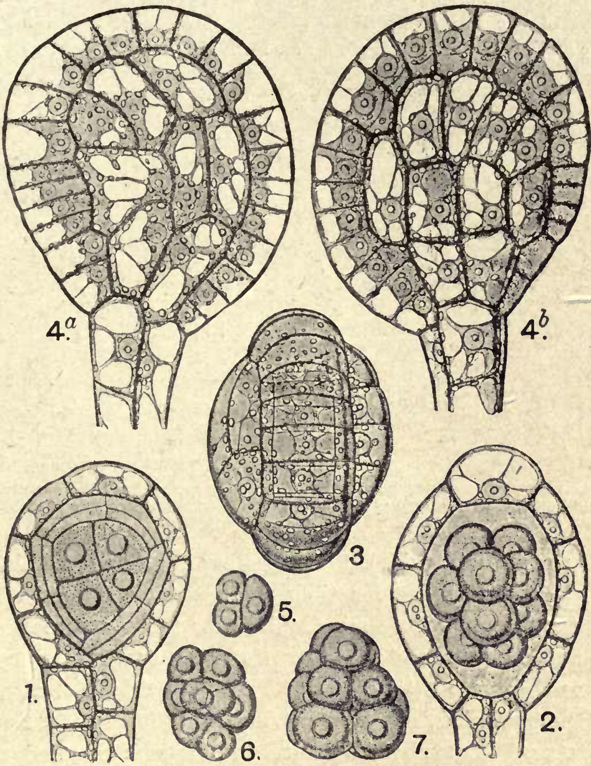


FIG. 280.
Later stages of development of the sporangium of *Nephrodium Filix-mas.* (After Kny.)

sporangium. Each spore-mother-cell then divides twice to form a *spore-tetrad*: in this process, just as in the formation of pollen-grains and other spores, the number of chromosomes is reduced to a half. Finally the resulting cells separate on ripening as individual *spores*, each covered by a protecting wall, rugged and dark brown at maturity. Owing to the absorption of the fluid contents of the sporangium the separate spores are dry and dusty, and are readily scattered. Since each of the 12 spore-mother-cells forms four spores, their number is 48 in each sporangium. Each mature spore consists of a nucleated protoplast, bounded by a colourless inner wall, and a brown epispore bearing irregular projecting folds.

Meanwhile the wall of the sporangium has differentiated into the thinner lateral walls of the lens-shaped head, and the annulus, which is a chain of about 16 indurated cells surrounding its margin (Fig. 280, 4*a*, 4*b*). These form a mechanical spring, which on rupture of the thin-walled stomium becomes slowly everted as its cells dry in the air, and then recovering with a sudden jerk throws out the spores to a considerable distance (Fig. 281). Dry conditions are necessary for this last phase of spore-production, viz. the dissemination of the numerous living germs. Each spore is a living cell, and may serve as the starting point for a new individual.

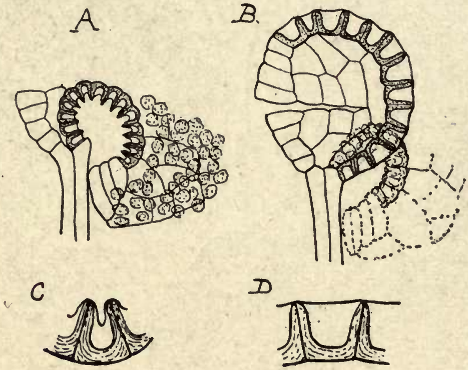


FIG. 281.
A = sporangium with annulus everted. *B*, a similar sporangium after recovery by a sudden jerk. *C*, condition of cells of the everted annulus. *D* = cells of annulus before evertion (see p. 133).

The dry conditions which are necessary for the dissemination of the spores do not suffice for their further development. Moisture and a suitable temperature are required for their germination. The outer coat then bursts, and the inner protrudes, cell-division appearing as the growth proceeds (Fig. 282). The body that is thus produced is called the *prothallus*, and it may vary in its form according to the circumstances. It usually grows first into a short filament attached by one or more rhizoids to the soil (4). It then widens out at the tip to a spatula-like and finally to a cordate form (Fig. 282, 5, 6). But when closely crowded the filamentous form may be retained longer (Fig. 284, 1). The body of the prothallus, exclusive of the downward-growing rhizoids, consists of cells which are essentially alike, arranged at first in a single-layered sheet. The peripheral parts retain this, but in the central region, below the emarginate apex, the cells divide by walls parallel to the flattened surfaces, and thus a massive central cushion is formed. The mature cells are thin-walled, with a peripheral film of protoplasm surrounding a central vacuole, and embedding the nucleus and numerous chloroplasts: intercellular spaces are absent (Fig. 15, p. 26). The whole body is thus capable of an independent physiological existence, nourishing itself by absorption from the soil, and by photo-synthesis (Fig. 283). But there is a large proportion of surface to bulk, and no serious resistance is offered to

FIG. 282.
Successive stages in germination of the spores of *Nephrodium Filix-mas*, to form the prothallus. (After Kny.)

the evaporation of water from it in dry air. Comparing the prothallus with the Fern-Plant as regards the water-relation, it is plainly less adapted for life on land, and more immediately dependent on moisture.

The prothallus thus constituted is capable in some cases of vegetative propagation by "gemmae." But this *gametophytic budding* is less common here than in the Bryophytes.

The dependence on moisture is still more obvious in the behaviour of the *sexual organs* which the prothallus bears. These are male and female, and they may be found on the same prothallus (Fig. 283), or on different prothalli (Fig. 284, 1). In the former case the *antheridia, or male organs,* commonly appear first, and the *archegonia, or female organs,* later. There may thus be a separation of the sexes either in time or in space. The flattened prothallus of the ordinary cordate type (Fig. 283) usually bears both sex-organs. When grown under normal circumstances on a horizontal substratum it produces them on its

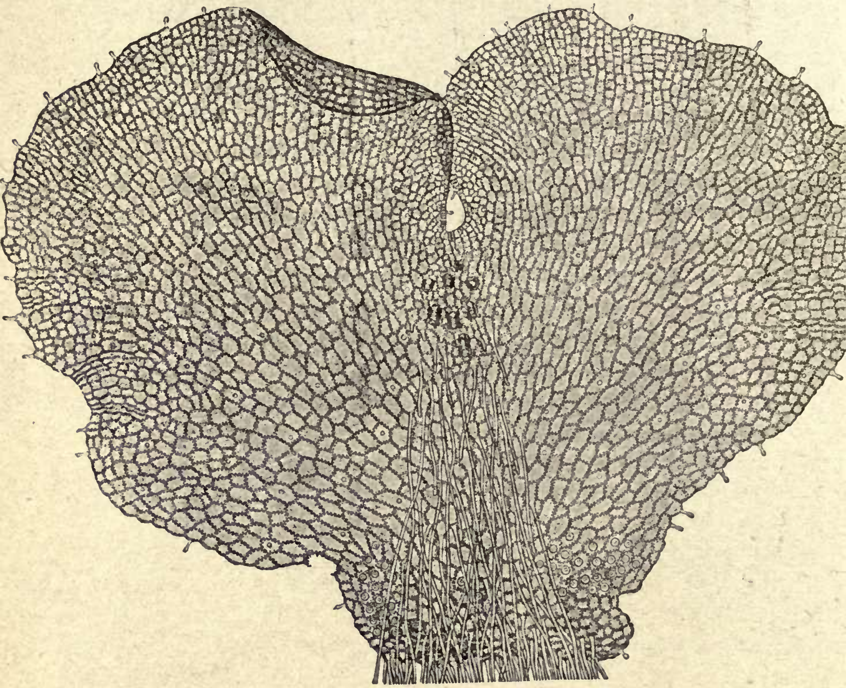


FIG. 283.
Mature prothallus of *Nephrodium Filix-mas*, as seen from below, bearing antheridia among its rhizoids, and archegonia near to the apical indentation. (After Kny.)

lower surface, the antheridia in the basal or lateral regions, the archegonia upon the massive cushion. The latter develop in acropetal order, the youngest being nearest to the incurved apex of the prothallus. The position of the sexual organs is evidently favourable to their continued exposure to moist air, or to fluid water which is necessary for carrying out their function.

The antheridium, which arises by outgrowth and segmentation of a single superficial cell (Fig. 284, 2, 3), consists when mature of a peripheral wall of tabular cells, surrounding a central group of *spermatocytes* (Fig. 284, 4, 5). The antheridium readily matures in moist air, but it does not open except in presence of external fluid water. This causes swelling of the mucilaginous walls of the spermatocytes, and increased turgor of the cells of the wall. The tension is relieved by rupture of the cell covering the distal end, and the spermatocytes are extruded into the water; in this the cells of the wall assist by their

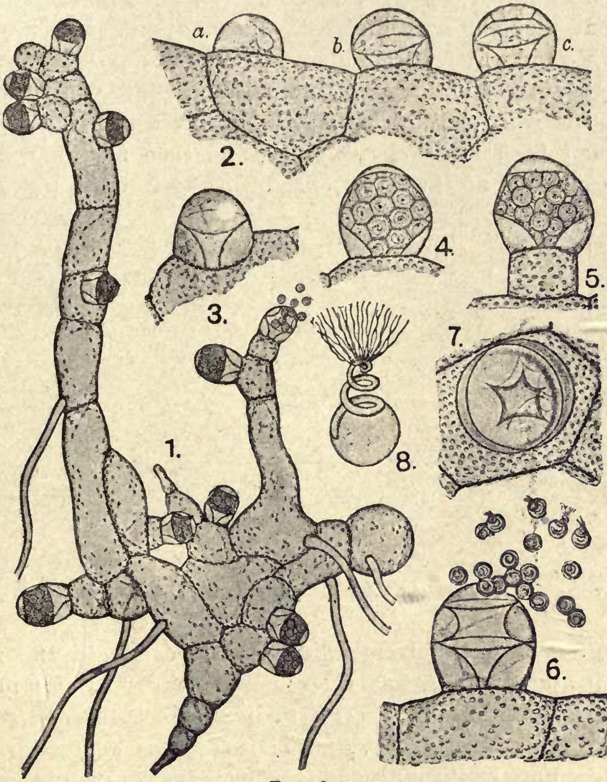


FIG. 284.
1, an attenuated male prothallus of *Nephrodium Filix-mas*. 2-5, stages of development of the antheridium. 6, 7, ruptured antheridia. 8, a spermatozoid highly magnified. (After Kny.)

swelling inwards, and consequent shortening (Fig. 284, 6). The spermatocytes thus extruded into the water which caused the rupture, soon show active movement, and the spermatozoid which had already been formed within each of them escapes from its mucilaginous sheath, and moves freely in the water by means of active cilia attached near one end of its spirally coiled body (Fig. 284, 8).

The archegonium also originates from a single superficial cell, and grows out so as to project from the downward surface of the thallus.

It consists when mature of a peripheral wall of cells constituting the projecting neck, and a central group arranged serially. The deepest-seated of these is the large *ovum*, which is sunk in the tissue of the cushion ; above this is a small *ventral-canal-cell*, and a longer *canal-cell* (Fig. 285, *A*). If prothalli be grown in moist air, and only watered by absorption from below, the archegonia will have no access to fluid water, and they will remain closed. Fertilisation is then impossible. But if they are watered from above, as they would be by rain in the ordinary course of nature, the external fluid water will bathe them, and rupture will result. This may be observed in living archegonia which have been kept relatively dry, and then mounted in water. The neck bursts at the distal end, owing to internal mucilaginous

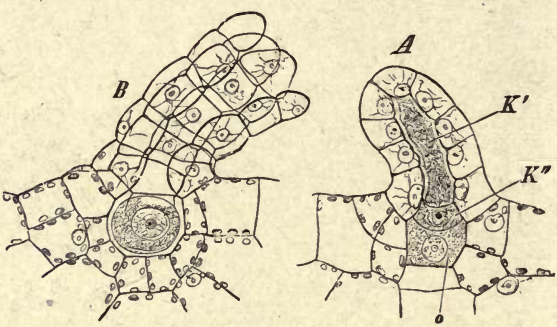


FIG. 285.
Archegonia of *Polypodium vulgare*. *A*, still closed. *o*=ovum. *K'*=canal-cell. *K"*=ventral canal-cell. *B*=an archegonium ruptured. (×240.) (After Strasburger.)

swelling, and its cells diverge widely. The canal-cell and ventral-canal-cell are extruded, and the ovum remains as a deeply seated spherical protoplast, while access to it is gained through the open channel of the neck (Fig. 285, *B*). Thus the same condition leads to the rupture both of the male and female organs. In nature a shower of rain would supply the necessary water, which would serve also as the medium of transit of the spermatozoids to the ovum. But the movements of the spermatozoids are not subject to blind chance. It has been shown that diffusion of a very dilute soluble substance, such as malic acid, into water serves as a guide, the spermatozoids moving towards the centre of diffusion. Probably it is in this way that they are attracted to the neck of the archegonium, which they may be seen to enter, and finally one spermatozoid coalesces with the ovum (Fig. 286). Fertilisation is effected by entry of the male nucleus into the female nucleus, and their complete fusion (Fig. 287). Thus the presence of external fluid water is essential for fertilisation in Ferns. Their normal life-cycle cannot be completed without it.

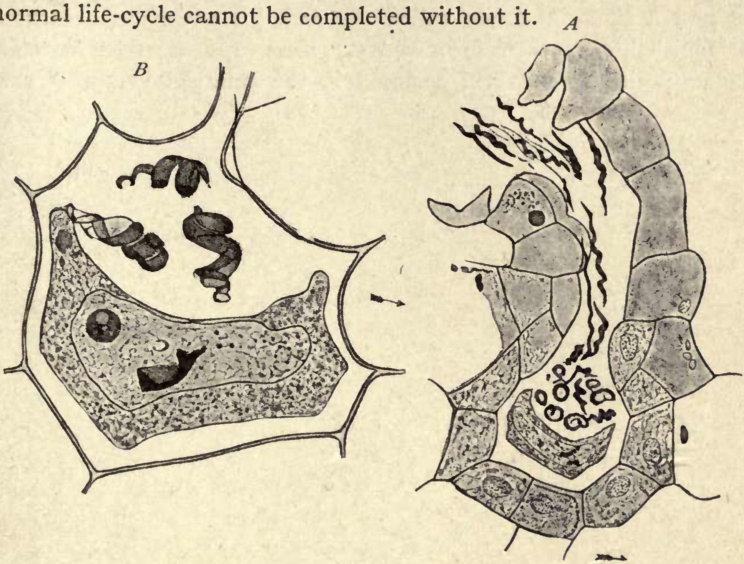


FIG. 286.

Fertilisation in *Onoclea sensibilis*: the arrows indicate direction to the growing point. *A* = a vertical section through an archegonium probably within ten minutes after entrance of the first spermatozoid. (× 500.) *B* = vertical section of the venter of an archegonium, containing spermatozoids, and the collapsed egg with a spermatozoid within the nucleus. Thirty minutes. (× 1200.) (After Shaw.)

The immediate consequence of fertilisation is growth and segmentation of the *zygote*, which first secretes a cell-wall. It divides into

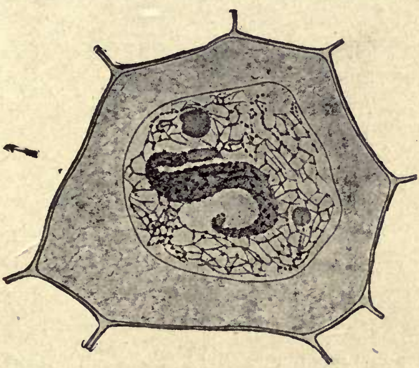


FIG. 287.

Horizontal section of an egg, showing coiled male nucleus within the female. Twelve hours. (× 1200.) (After Shaw.)

octants, four of which constitute an *epibasal hemisphere*, directed towards the apex of the parent thallus, giving rise to *axis* and *leaf* of the sporeling; four form a *hypobasal tier*, which gives rise to the first *root* and a suctorial organ called the *foot*. These parts are soon distinguishable by their form and structure, and are seen in their relative positions, but still enclosed in the enlarged venter of the

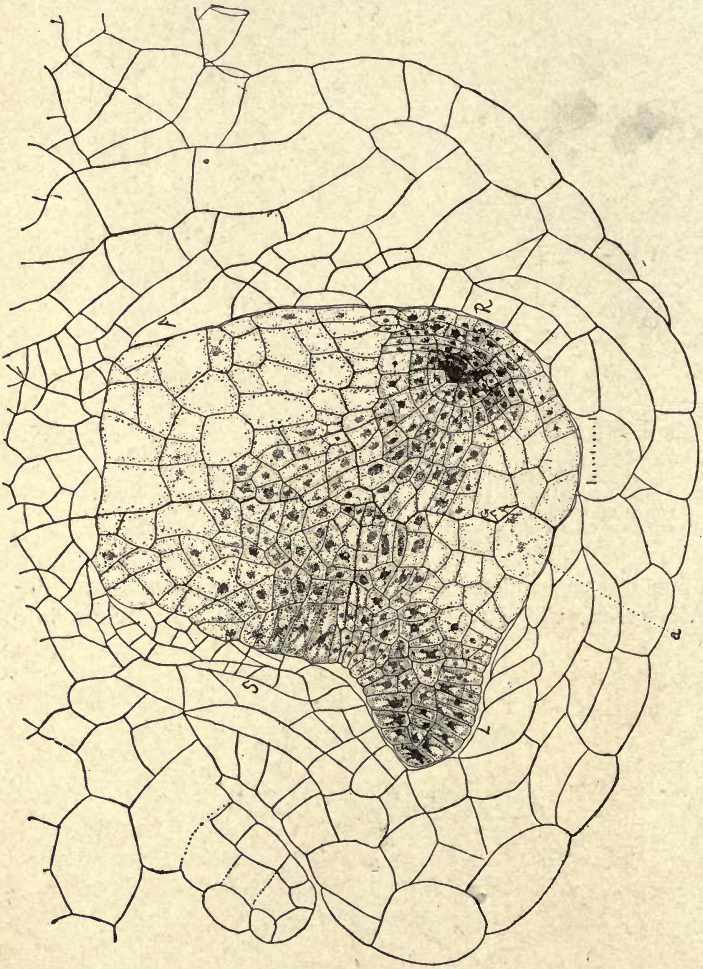


FIG. 288.
Embryo of *Adiantum concinnum* in the enlarged venter of the archegonium, so far advanced as to show the parts of the embryo. The epi-basal hemisphere is to the left, the hypobasal to the right. *L*=leaf or cotyledon. *R*=root. *S*=stem. *F*=foot. (After Atkinson.)

archegonium, in Fig. 288. Soon the cotyledon and first root burst their way out: the former expands as the first nutritive leaf, the latter buries itself in the soil (Figs. 289, 290). At first the young Fern-Plant is dependent upon the prothallus that encloses it, but by means of its cotyledon and its root it soon becomes self-dependent, and the prothallus rots away. It is then only a matter of time and opportunity for it to attain characters similar to those of the parent Fern-Plant.

These are the salient features in the life-cycle of a Fern as it is seen in its simplest form. They may be represented graphically to the eye in a diagram (Fig. 291). The two most notable points are those where the individual is represented only by a single cell, viz. the *spore*, and the *zygote*. These are two landmarks between which intervene two more extensive developments, on the one hand the sexual generation or prothallus, on the other the spore-bearing generation, or Fern-Plant. If the events above detailed recur in regular succession the two phases of life will alternate. Of these the one bears sexual organs, containing sexual cells or gametes, and it may accordingly be called the *gametophyte*; the other is non-sexual, but bears sporangia containing the spores, and is accordingly called the *sporophyte*. The study of Ferns, and of Pteridophytes at large, leads to the conclusion that this regular alternation is typical for them all. These two alternating generations differ not only in form but also in their relation to external circumstances, and especially in the water-relation. The sporophyte is structurally a land growing plant, with nutritive, mechanical, and conducting tissues, and a ventilating system. Not only is it capable of undergoing free exposure to the

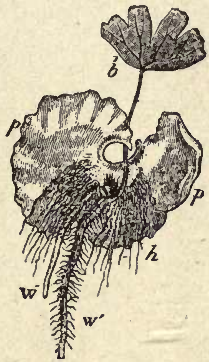


FIG. 289.
Adiantum Capillus Veneris. The prothallus, *pp*, seen from below has a young Fern-plant attached to it. *b* = first leaf. *w*, *w′* = first and second roots. *h* = root hairs of the prothallus. (× about 30.) (After Sachs.)

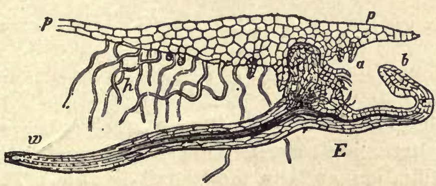


FIG. 290.
Adiantum Capillus Veneris. Longitudinal section through the prothallus, *pp*, and young Fern-plant E. *h* = root hairs of prothallus. *a* = archegonia. *b* = the first leaf. *w* = the first root of the embryo. (× 10.) (After Sachs.)

ordinary atmospheric conditions, but dryness of the air is essential for the final end of its existence, viz. the distribution of its spores. On the other hand, the gametophyte is structurally a plant ill-fitted for exposure, with undifferentiated and ill-protected tissues and no ventilating system, while the object of its existence, viz. fertilisation, can only be secured in the presence of external fluid water. As regards the water-relation the whole life-cycle of a Fern, or of Pteridophytes generally, might not inaptly be designated as *amphibious*, since the one phase is dependent on external fluid water for achieving its object of propagation, while the other is independent of it.

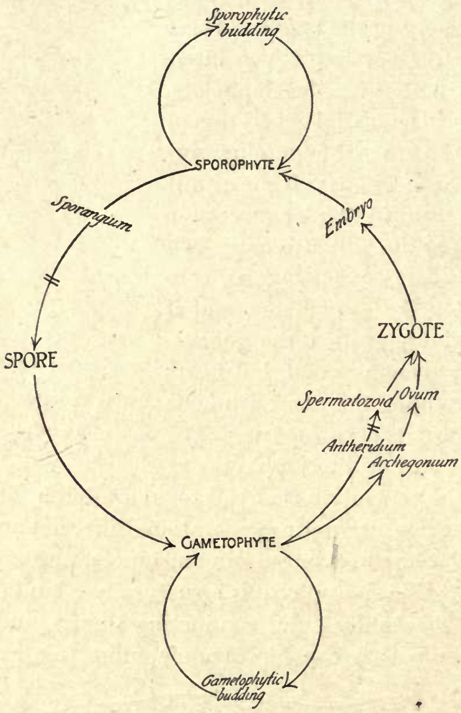


FIG. 291.
Diagram illustrating the cycle of life of a Fern.

The normal cycle thus presented to the eye involves differences of nuclear condition of the alternating phases, those differences being established respectively by fertilisation and by the tetrad-division. The *sporophyte* or Fern-Plant is *diploid*, and the number of chromosomes is usually very large (about 90 for *Athyrium*, 144 for *Lastraea pseudo-mas*, but only 32 for *Marsilia*). This number is reduced to one half in the tetrad-division of the spore-mother-cells, and the spores on germination produce the *gametophyte* which is *haploid*. But in fertilisation, when the gametes fuse, the diploid number is restored. This normal cycle corresponds to that seen in higher forms, the substantive Plant being in all cases the diploid sporophyte.

The cycle as thus defined is liable to certain modifications. Some are by the introduction of new incidents, others by the excision of certain phases. For instance, buds may be produced either on the Fern-Plant or on the prothallus, which repeat respectively the one or the other (Fig. 277, p. 336). These are merely amplifications of the *soma*, without any change of constitution of

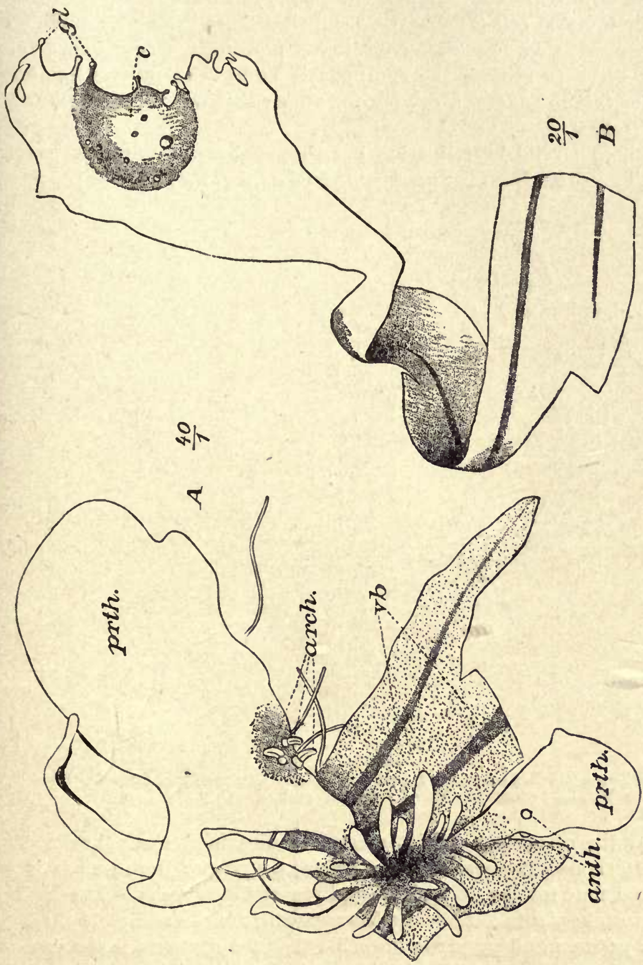


FIG. 292.

A, part of a pinnule of *Athyrium Filix-foemina*, v. *clarissima*, showing vascular bundles (*vb*); from the position of a sorus numerous prothalli have grown out, not derived from spores (apospory), bearing antheridia, and archegonia. *B*, tip of a pinnule of *Polystichum angulare*, v. *pulcherrimum* (×40), which has grown out directly into a prothallus. *c*=cushion. *gl*=glands. (×20.)

the tissues, or of the nuclei. But others are of the nature of short-cuts. For instance, a prothallus may arise from the Fern-Plant without the intervention of spores (apospory), as in certain forms of *Athyrium* or *Polystichum* (Fig. 292, *A*, *B*). Or a Fern-Plant may spring directly from a prothallus without the sexual process (apogamy), as in *Pteris cretica* (Fig. 293). Such examples show that the events of the life-cycle are not immutable. But they raise difficulties of interpretation in terms of chromosomes.

In the relatively simple case of *Nephrodium pseudo-mas*, var. *polydactyla* a young sporophyte is produced as a direct outgrowth from the prothallus. By a careful examination of the bud-forming tissue it has been found that the bud is preceded by a sort of irregular fertilisation. The nucleus passes from one cell through a pore in the cell-wall into the next cell. There it fuses with the nucleus of the invaded cell (Fig. 294). Doubtless there is here a doubling of the chromosomes, as in normal fertilisation; and such a cell, like a false zygote, may serve to initiate the sporophytic bud. The process has been styled *pseudomixis* to suggest a comparison with sexuality, while marking its distinctness from it.

In other cases careful investigation has shown that a gametophyte may be diploid. Transition from one generation to the other may then be repeated,

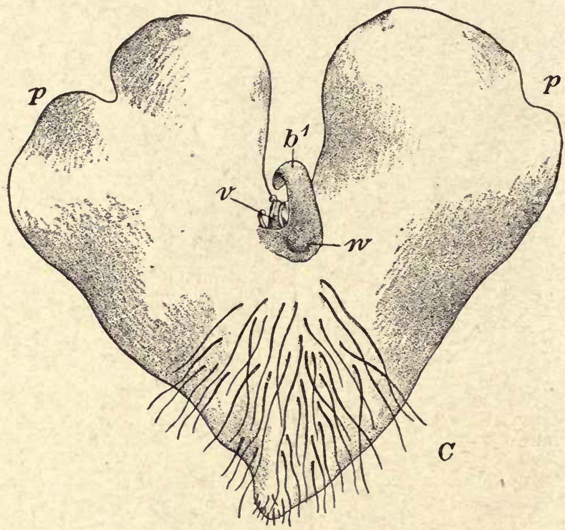


FIG. 293.
Pteris cretica; prothallus seen from below, bearing an apogamous bud derived not by fertilisation but by direct growth from the cushion. (After De Bary.)

while uniformity of chromosome-number is maintained throughout. This is seen in *Athyrium filix-foemina*, var. *clarissima*, where the number is 90, approximately that for the normal sporophyte of that species. The same is the case for certain plants of *Marsilia Drummondii*, which are diploid throughout, with 32 as the number. It is probable that the converse is the case for *Lastraea pseudo-mas*, var. *cristata* (Fig. 295), for the chromosome-number throughout was found to be variable, from 60 to 78, while in that species the normal number for the sporophyte is 144. Not only do such cases show that the usual chromosome-cycle may be departed from, but also that the external characters are not directly dependent upon the chromosome-number.

The cycle of life of a Fern shows more clearly than that of any of the Vascular Plants hitherto described the antithesis of the two generations which constitute it. Either can grow, nourish itself, and even multiply independently of the other. It is true that the young sporophyte is nursed temporarily in the parent prothallus. But this is only a transient event and is soon over. A similar nursing period, with much greater adaptive detail that lends added efficiency, is seen in the Seed-Plants. The main difference between the Seed-Plant and

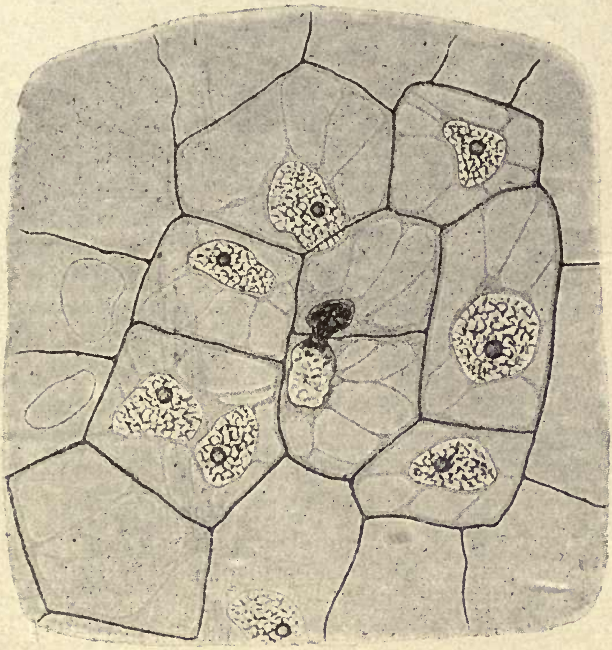


FIG. 294.
Nephrodium pseudo-mas, var. *polydactylum*. Tissue of prothallus where an apogamous growth is to be found, showing on the left a cell with two nuclei, while an adjoining cell has none. At the centre a nucleus is seen passing through a perforation of the wall, and fusing immediately with that of the cell it enters. (After Farmer, Moore, and Miss Digby.)

the Fern lies in their spores. The former are *heterosporous*, the latter are few exceptions) *homosporous*. The advantage of the large female spore is that it contains already a supply of nourishment for the young germ after fertilisation, so that a vegetative prothallus is not necessary. Especially is this so in Seed-Plants where the spore is retained in the tissue of the parent, and can draw nourishment continuously from it. On the other hand, in the primitive homosporous state the individual spore is small and is cast out to fend for itself. It is then incumbent on the spore, when it germinates, at once to increase its slender store, otherwise it cannot produce gametes, or nourish the resulting germ. Hence the independent vegetative existence of the gametophyte.

FIG. 295.
Nephrodium pseudo-mas, v. *cristata* (Cropper). Drawing by Dr. Lang showing apogamous transition from prothallus to sporophyte, and subsequent aposporous transition to prothallus at the apex and margins of the leaf.

Further, the difference in biological relation of the two generations to water is very marked. The prothallus, which is semi-aquatic, is the less prominent, and its growth is normally limited in size and duration. The Fern-Plant, which is definitely terrestrial in structure and function, is in the ascendent, and its growth is unlimited in size and in duration. A Fern is like a man with one foot in the water and one on land. But the foot that is on land is more firmly set than the other.

DIVISION IV.

BRYOPHYTA.

CHAPTER XXII.

MUSCI AND HEPATICAE: MOSSES AND LIVERWORTS.

THE Bryophytes include two Classes, represented by very numerous species, widespread in all lands except in those of persistent drought. They are the *Musci* or *Mosses*, and the *Hepaticae* or *Liverworts*. These form a very natural alliance, and indeed are distinguished from one another only by minor characters. Everyone knows the general appearance of Mosses, as low-growing leafy plants, chiefly found in moist surroundings. But Liverworts, with a similar habitat, have commonly a flattened form, sometimes without obvious leaves, described as a thallus. Thus the Bryophytes may be either *leafy* or *thalloid*.

All the Bryophytes show a cycle of life of the same general plan as that of the Pteridophytes, having like them two alternating generations. The chief difference lies in the proportions and behaviour of these two phases. It has been seen in Ferns how the Sporophyte has obtained a firm hold on the Land, where it is rooted, and leads an independent life as the "Fern Plant," while the prothallus or gametophyte is relatively small. But in all the Bryophytes, that green and often leafy structure which is recognised as the "Moss or Liverwort-Plant" turns out on examination to be the *gametophyte*. It bears the sexual organs, while the *sporophyte*, which is produced from them and bears the spores, is the well-known *Capsule*, or *Sporogonium* (Fig. 296). In all the Bryophytes the spore-bearing generation is dependent upon the gametophyte throughout its existence. It never fixes itself directly in the soil as the Fern-Plant always does. Thus the leading morphological feature is *the relatively high vegetative development of the*

FIG. 296.
Catharinea (*Atrichum*) *undulata*. The leafy gametophyte, or Moss Plant, bearing capsules, or sporogonia, which are the dependent sporophyte generation. (After Schimper.)

sexual generation, which is able to carry on active nutrition and propagation, and commonly persists as a perennial.

Physiologically also there is this difference from Vascular Plants, that there is no elaborated root-system. It is true Mosses and Liverworts have rhizoids, but they depend for their water-supply not only upon localised absorption by these, but also upon general absorption by their whole surface, as opportunity offers for it.

MUSCI, OR MOSSES.

Mosses are usually gregarious. The leafy plants are often massed together in tussocks or cushions with their small stems upright, and occasionally branched. Or they may be isolated and straggling, with more frequent branchings. They are fixed in the soil or some other substratum by numerous rhizoids springing from their base (Fig. 297), or from a creeping rhizomatous shoot from which the upright stems arise (Fig. 296). Their stature is never great, and often they are very

FIG. 297.
Lower part of stem of a Moss (*Barbula muralis*) with protonema. *a-b* shows the soil-level. *B* is a young gemma. *kn*=a bud that would grow into a new plant. (After H. Müller.)

minute. Though they are commonest where moisture is plentiful, and sometimes grow actually in water (*Fontinalis*), or along its edge (*Porotrichum alopecurum*), they often flourish in stations apparently the most unpromising, such as exposed rocks or roofs, tree-trunks, and wall-tops. Here they may be dried to crispness in summer. But they recover at once after a shower of rain. This capacity of resisting drought, and of instant recovery by surface-absorption of water, is one of the causes of their biological success; for by entering thus a state of physiological inhibition, they can tide over extreme conditions.

The best way of presenting the life-history of a Moss is by starting from the spore shed from the ripe capsule. The spores are so minute that they are readily carried as dust by the breeze. A striking instance of their ubiquity is seen where ashes are left after a fire in woods, or even on cinder paths. A certain Moss, *Funaria hygrometrica*, commonly makes its appearance there, though none of the species may be seen in the near neighbourhood. But occasionally the method of spread is more precise. Thus the spores of some Mosses are sticky, and readily carried by insects. This is so with the dung-infecting *Splachnum*, the agent of its spread being the dung-fly. Scattered in one way or another, the spore germinates in presence of moisture, giving rise to filaments, which as they grow are partitioned into cells, and soon branch. Some of the branches are exposed at the surface of the soil, and develop chlorophyll. Others burrowing into

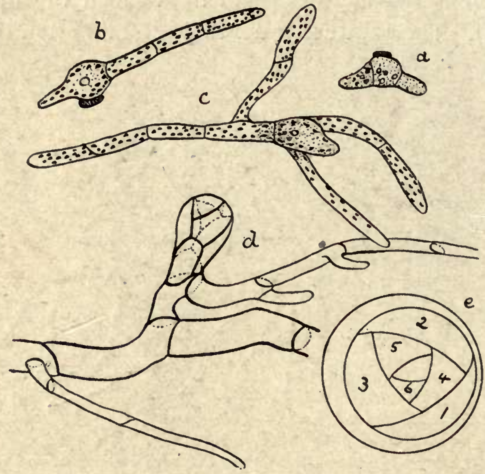


FIG. 298.

a, b, c, **germination of Moss-spores to form protonema. *d*=formation of a bud laterally upon the protonema. *e*=diagrammatic plan of the segmentations of *d*, as seen from above. (After H. Müller.)**

the soil are colourless, or have brownish walls ; they serve as rhizoids (Fig. 298). The filamentous system thus produced is called *protonema*, and the formation of Moss-Plants is regularly preluded by this filamentous stage. If grown in dim light it may increase indefinitely, but with full exposure it sooner or later forms Moss-plants. These arise as buds, each taking the place of a branch of the protonema, and may be held to be a condensed form of it. The segmentation of the bud is from an initial cell, by walls with rather more than 120 degrees of divergence, as shown in ground plan (Fig. 298, *d, e*). Each segment gives rise to a leaf of the Moss-Plant, borne on the upward-growing stem. But this does not check the growth of the protonema, which may extend indefinitely. Branches from the rhizoids may anywhere rise above ground, also forming new buds (Fig. 297). In this way the usual gregarious habit is established.

In the smaller Mosses the structure of the leafy Plant is very simple. The leaves may consist only of a single layer of green cells (Fig. 72, p. 100), with a strand of elongated cells forming a central vein, which stops at their bases: the stem is here traversed by an independent conducting cord (*Mnium*). But in *Polytrichum*, and other large Mosses, there is a conducting system consisting of a central column of water-conducting tissue, upon which strands from the leaves are

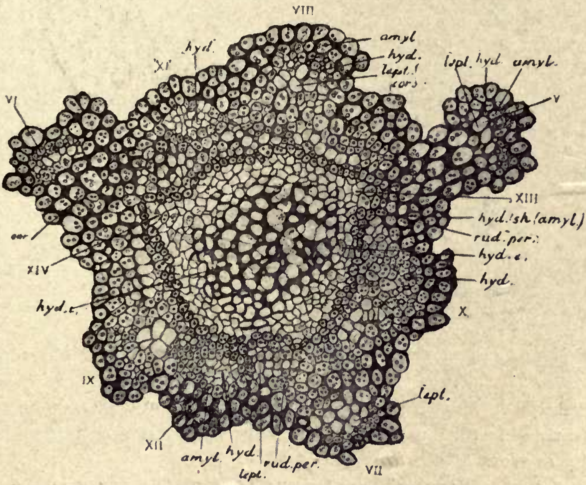


FIG. 299.

Transverse section of the central tissues of an aerial leafy stem of *Polytrichum commune*, showing entry of leaf-traces into the mantles of the central cylinder. The leaf traces are numbered from without inwards. *amyl* = starchy parenchyma. *hydr* = hydrom. *lept* = leptom. *hyd. sh.* = hydrom-sheath. *rud. per.* = rudimentary pericycle. × 200. (After Tansley and Chick.)

applied. Each of these consists of hydrom (xylem) and leptom (phloem) (Fig. 299). Thus in the gametophyte of the larger Mosses a structure is seen which offers an analogy with that of the sporophyte of Vascular Plants.

A curious structure is seen in the leaves of *Polytrichum*, and some other Mosses, which is probably effective in collecting and retaining water during rain. The flat blade bears on its upper face numerous longitudinal plates of chlorophyll-parenchyma, sometimes overlapped by the membranous margins of the leaf. In *P. commune* (Fig. 300) the distal cells of each plate are enlarged, so that its chlorophyll-cells abut upon an almost closed space. As the leaf flattens when moist, and curls its margins upwards when dry, the access of atmospheric air to the parenchyma is controlled as it is by the automatic stomata in Vascular Plants. But this is only an analogy, for the surfaces of the lamellae are actually the outer surface of the leaf thrown into deep folds, and the leaf itself is part of the gametophyte, not of the sporophyte.

An example in the Moss-Plant of extreme simplicity is seen in *Buxbaumia*, which habitually grows on humus soil, or rotting tree-stems. Its male plant consists of only a single hollowed leaf, surrounding an antheridium. The female consists of a few leaves, and neither are green. There is an extensive green protonema, but the rhizoids show a hypha-like habit, and establish very close relations with the humous substratum. The sporogonium itself is

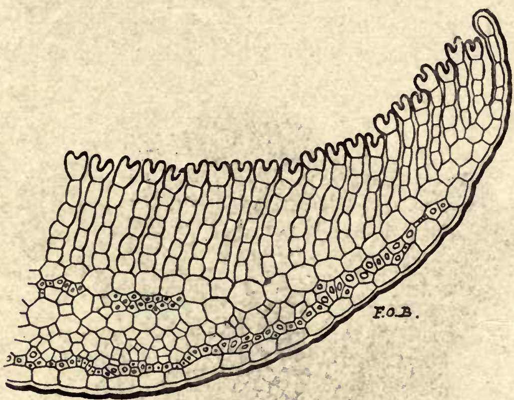


FIG. 300.
Half of a transverse section of a leaf of *Polytrichum commune*, showing the longitudinal plates cut in section.

relatively large in *Buxbaumia*. The evidence of *saprophytism* is strong, and it seems probable that many Mosses share that mode of irregular nutrition in varying degree.

Among the many special adaptations seen in the gametophyte of Mosses one of the most peculiar is that of the Bog-Mosses (*Sphagnum*): it is shared in some degree by the quite distinct genus, *Leucobryum*. The tissues of stem and leaf include not only living cells with active protoplasts, but also dead cells of larger size, with their walls propped out by annular or spiral fibrous thickenings, and opening by round pores to the outside. They form a capillary system by which water is retained as in a sponge. It is this structure which gives *Sphagnum* its value for surgical dressings. These Mosses occupy large areas under cold wet climates, and their dead bodies are the chief constituent of *peat*.

The permanent establishment of new Moss-Colonies is largely due to the profusion of their methods of vegetative propagation. *Protonema* is a regular preliminary to the formation of Moss-Plants. A filament may arise from any undamaged cell, either of the plant itself or of the protonema. If a sod on which Mosses are growing is inverted and kept moist, protonema and ultimately a new crop of Moss-Plants will arise from the rhizoids already there. If leaves or stems be chopped up, any undamaged cell may grow out under favourable circumstances into protonema, giving rise to a new crop. But besides this, in many Mosses certain parts are so developed during normal life that they are readily detached as *gemmae*, which may start new colonies in fresh stations. The protonema itself may break into short lengths (*Funaria*), or bulbils may be formed upon it (*Barbula*) (Fig. 297, *B*), or gemmae may be formed on the surface or the leaves (*Grimmia*), or in terminal cups (*Tetraphis*). Or whole leaves, slightly

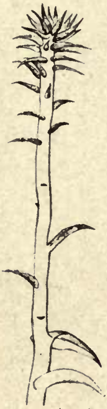


FIG. 301.
Leaf gemmæ of *Aulacomnion palustre.* The drawing shows the gemmæ, and scars where some have been shed.

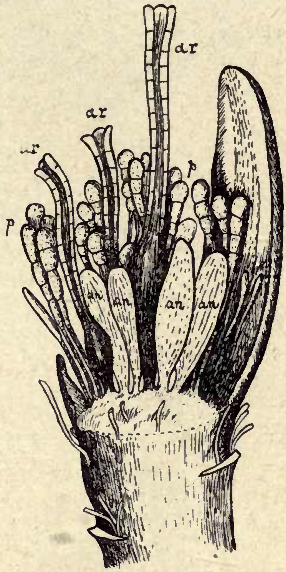


FIG. 302.
Meesia uliginosa, Hedw. (After Hedwig, 1787.) Showing antheridia (*an*), and archegonia (*ar*), with paraphyses (*p*), on same axis.

modified for the purpose, may be detached, as in *Aulacomnion palustre* (Fig. 301). In any case protonema is formed first, and subsequently Moss-Plants.

Frequently it is by such means that Mosses are spread. But a more certain transfer to longer distances is by the minute *spores* produced in the capsule, or *sporogonium*, which thus reveals itself as the *sporophyte generation* (Fig. 296). This like other sporophytes results from propagation by sexual organs borne by the gametophyte. The antheridia and archegonia of Mosses are similar in essentials to those of Pteridophytes, but different in details. They are sometimes borne on the ends of the main stem (acrocarpic), sometimes on short lateral branches (pleurocarpic), and this character is useful in the classification of Mosses. The sexual organs are often protected by specially developed "perichaetial" leaves, which give an almost flower-like appearance (*Polytrichum*). In some Mosses the antheridia and archegonia are grouped together, as in *Meesia* (Fig. 302); but commonly they are separate, either on distant branches of the same plant (*Funaria hygrometrica*), or on different plants (*Polytrichum*, *Buxbaumia*).

The analogy between the arrangement and distribution of the stamens and carpels in the flowers of Angiosperms and the sexual organs in the peri-

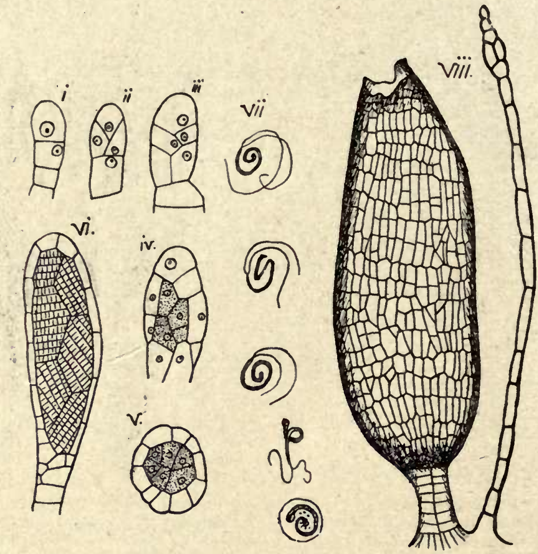


FIG. 303.
i.-vi. Stages in development of the antheridium of *Funaria hygrometrica*, after Campbell (×400). vii. Spermatozoids of *Funaria*, after Campbell, and Sachs. (×800). viii. Empty antheridium of *Andreaea*, with paraphysis, after Kühn. (×135).

chaetia of Mosses is obvious. But it must always be remembered that the two sides of this comparison are essentially different. The antheridia and archegonia of Mosses are the real sexual organs borne by the gametophyte and they contain the gametes; the ovules and pollen-sacs of Angiosperms are parts of the sporophyte, specialised so as to produce the highly modified gametophytes, which in their turn produce the gametes.

Both types of sexual organs project freely from the surface of the plant. Each originates from a single cell, by a segmentation which shows a continued apical sequence, and is quite distinct from that seen in the sexual organs of Pteridophytes. The *antheridium* (Fig. 303, i.-viii.)

is a club-shaped body, seated on a short massive stalk, and it is frequently large enough to be seen by the naked eye. It consists of a peripheral wall of tabular cells, covering a mass of cubical spermatocytes (vi.). It bursts when ripe at the distal end (viii.). There is often a special cap of mucilaginous cells which produce and control the pore of exit. The spermatozoids can then escape in a thin stream, embedded in mucilage from which they soon escape. In cases where

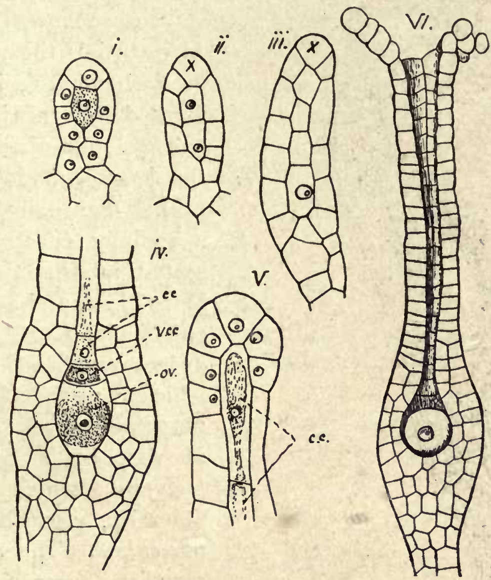


Fig. 304.

i.-v. Stages in development of the archegonium of *Funaria*, after Campbell (× 400). vi. Mature archegonium of *Andreaea*, after Kühn (× 250). i. shows cover-cell separated from central-cell (shaded.) ii. iii. cover-cell (x) undergoing segmentation as an initial cell, giving rise to three rows of lateral and one of basal segments: the former constitute the "neck," the latter are the canal cells. iv. shows the ovum (*ov*), ventral canal cell (*v.c.c.*), and canal-cells (*c.c*). *V*. shows the apex of the neck before rupture, with canal-cells (*c.c.*) within.

the perichaetial leaves face upwards, a shower of rain would bring the rupture about, and the mucilaginous contents may be seen and collected on a slide in a drop of water. The biciliate *spermatozoids* may then be observed in active movement (Fig. 303, vii.).

The *archegonium* is a flask-shaped body with a long neck (Fig. 304). It is seated on a massive stalk, and it also arises from a single superficial cell. When mature it consists of a peripheral wall, which in the lower ventral portion is double, but the neck consists of a single layer built up of six rows of cells, as against four in the Pteridophyta. The wall encloses a central series, consisting of canal cells (*c.c.*) which may sometimes be very numerous, a ventral-canal-cell (*v.c.c.*), and the ovum (*ov.*). At maturity the end of the neck opens in presence of water, owing to pressure of mucilaginous swelling within; a funnel-like channel then leads down to the ovum (Fig. 304). Spermatozoids, motile in the water, may be seen to enter it, and there is reason to believe that their movements are directed by diffusion from it of some soluble substance, such as cane sugar. In essentials the process is as in Peridophytes, but there is marked difference in the details.

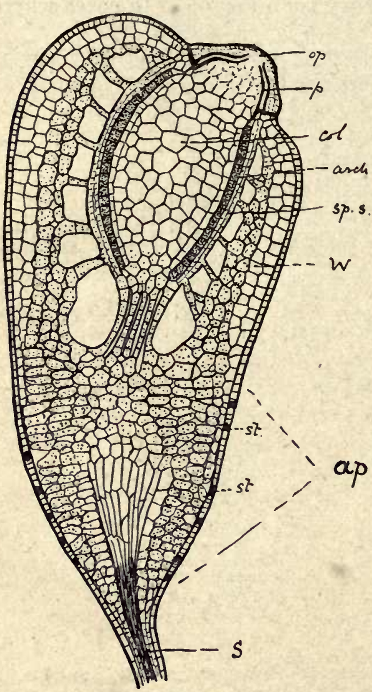


FIG. 305.

Median section of an immature sporogonium of *Funaria*. *s*=seta. *ap.*=apophysis. *w*=water storage tissue. *st.*=stomata. *sp. s.*=spore-sac. *arch.*=archisporium. *col*=columella. *p*=peristome. *op*=operculum. Based on a drawing by Haberlandt. (× 20.)

The result of fertilisation is the *Sporogonium* (Fig. 296, p. 354). It usually appears as a radially constructed body, seated in the tissue of the Moss Plant, and bearing at the end of a long stalk (*seta*) a more or less oval head (the *capsule*), which at ripeness contains very numerous spores. It is covered at first by a hood or cap (*calyptra*), which falls off at maturity, disclosing a lid, or *operculum*. This finally separates by a transverse split, and falling away opens the capsule, just as the lid might be taken off a covered jar. In most Mosses a fringe of ragged filaments, the *peristome*, is thus disclosed, which by their hygroscopic movements serve to distribute the dry and dusty *spores* (Fig. 308). The sporogonium is usually green while young, but yellowish or brown when ripe. This is due to photo-synthetic tissue, which is specially developed at the enlarged base of the capsule (*apophysis*), where also stomata may be found, providing for ventilation (Fig. 305). But such tissues dry up at maturity, so that the capsule is then full of the yellowish spores.

The sporophyte thus constructed differs from all the sporophytes hitherto described, in being *dependent* throughout its existence upon the gametophyte; in the *absence of any appendages*, and normally of any branching whatever; also in the fact that *the spores all originate from one continuous spore-sac* contained in the capsule, and not from separate sporangia. These features are common for the Bryophyta, and mark a simpler grade of evolution of the diploid generation. Whether this is a primitive simplicity, or a consequence of reduction, is a question which can only be discussed on grounds of broad comparison. But the probability is that it is primitive.

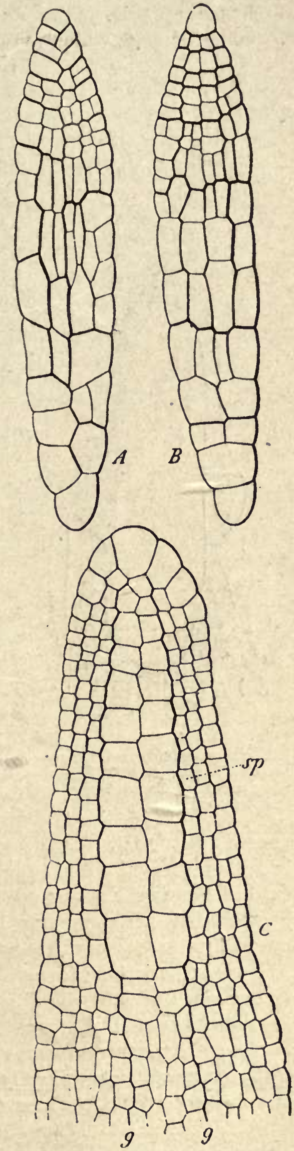


FIG. 306.
Ceratodon purpureus (after Kienitz-Gerloff). *A*, *B*, young embryo seen from points of view at right angles to one another. *C*=an older embryo. *gg*=outer limit of the endothecium. *sps*=outer spore-sac.

The Moss Sporogonium is without any of those lateral appendages which are so conspicuous a feature in Vascular Plants. Its external form contrasts with theirs in being simple. It is essentially a spindle, with polarity defined as apex and base. Transverse expansion will then account for the origin of the capsule on the end of the seta. But this capsule is a complicated body in the higher Mosses. Its complexity arises from an advance in internal structure, which thus replaces elaboration of external form. To understand it the best approach is through development.

The zygote first divides by a basal wall, which is transverse or slightly oblique to the axis of the archegonium. This at once defines the polarity. It is succeeded by a brief apical growth in the epibasal half, with a two-sided apical cell. The hypobasal half also segments, but less regularly, boring its way downwards into the tissue of the parent (Fig. 307). A spindle-shaped body is thus produced (Fig. 306, *A*, *B*). Subdivision of the segments gives a central tract (endothecium), and a peripheral tissue (amphithecium) (Fig. 306, *C*). The former is the exclusive source of spore-formation; the latter produces the external tissues of the wall, parts of which are photo-synthetic while young. Thus far the sporogonium is enclosed in the growing venter of the archegonium (Fig. 307). As it develops further the lower part remains thin, forming the seta, which may be traversed by a conducting strand (Fig. 305). But the distal part enlarges to form the capsule. A layer of cells is there cut off from the periphery of the endothecium, and acquires dense contents. This is the *archesporium*, which is shaped like a barrel without ends (*arch.* Fig. 305). Within it is the large-celled water-storage tissue of the columella. The amphithecium, limited now by a superficial epidermis with stomata, forms a lacunar photo-synthetic tissue, with a large and continuous air-space outside the archesporium. This tissue is specially active in that region called the apophysis, where the stomata are most frequent. In some Mosses it is enlarged as a very effective organ of nutrition.

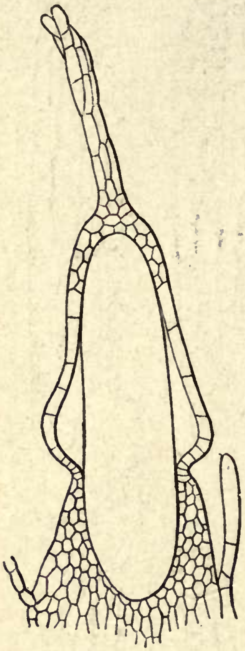


FIG. 307.
Young sporogonium of *Physcomitrella patens*, shortly before the rupture of the archegonial wall. (After Hy.)

As the development proceeds the cells of the archesporium divide repeatedly, forming a thick cylinder of *sporogenous cells* surrounding the columella, and limited externally by a double layer of cells of the amphithecium. This constitutes the *spore-sac*. The cells then separate, and rounding off in a fluid that fills the sac, each undergoes *tetrad-division*, and finally produces four spores. *Reduction* takes place as usual, common numbers of chromosomes for Mosses being 12-6. The numbers are low for Bryophytes generally. The mature spore is very minute, and almost spherical, and it contains globules of oil.

Meanwhile above the fertile region certain inner cells of the amphithecium undergo changes of induration of the cell-walls to form the *peristome*, which is closely related to the liberation of the spores (Fig. 305). As its structure differs in detail in various Mosses, it provides facts valuable in their classification. The case of *Fontinalis* serves as a good example of a complicated peristome, as it is seen after the operculum falls away. It is double (Fig. 308). The inner peristome forms a sort of connected lattice-work which will allow the spores singly through its pores, but prevents them all falling out at once. The outer consists of 16 teeth, which are really strips of thickened cell-wall, separated from one another by the breaking down of the thinner lateral connections. They show movements with changes of moisture in the air, and catching one on another by their rough edges, they give flicking movements on release, which throw the spores to a distance. The spores thus shed germinate to form protonema, as seen above (Fig. 298).

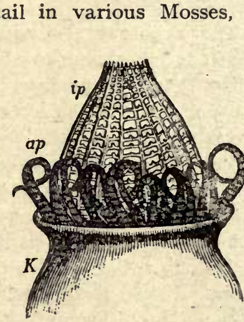


FIG. 308.
Fontinalis, apex of capsule (*K*) after shedding the operculum. *ap*=outer peristome. *ip*=inner peristome. (After Schimper.) (×50.)

Hepaticae or Liverworts.

The Life-Cycle of Liverworts is on the same plan as that of the Mosses, the gametophyte being the predominant generation. In the simpler types it is thalloid, and may be forked. *Pellia*, which is common on moist clay banks, is constructed like a large Fern prothallus, but more fleshy. Most Liverworts, however, bear appendages. Thus the thalloid *Riccia* has scales upon the ventral (lower) surface of its fleshy thallus. Its upper surface is deeply penetrated by narrow air-canals, each bounded by four rows of chlorophyll-containing cells, of which the outermost may be enlarged. The result is a ventilated photo-synthetic structure. In the series of the Marchantiales this ventilated construction is further developed, so as

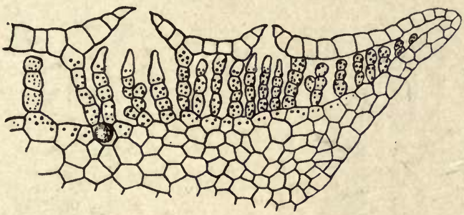


Fig. 309.
Vertical section through part of the thallus of *Targionia*, showing the cavities opening by pores on the upper surface, and containing filaments of chlorophyll-cells. (× 75.)

to render the thallus very efficient for photo-synthesis on land. For instance, in *Targionia* (Fig. 309), the flattened thallus, bearing ventral scales below, and fixed by rhizoids in the soil, is differentiated into a massive lower region chiefly for storage (though it is also penetrated by a mycorhizic fungus through the root-hairs), and an upper photosynthetic region marked by large, overarched air-chambers. Each of these communicates with the outer air by a large pore, which is more or less under control. From the floor of the chamber arise active green cells, grouped in simple, or branching filaments. Such developments, with varying detail, are characteristic of the Marchantiales. The analogy with Angiospermic leaves is obvious, but the origin of the structure is here quite different, being chiefly due to surface-involution.

A distinct line of vegetative advance is shown by the Jungermanniales, in which successive steps may be found from the thalloid state, through various forms of marginal lobes, to a full leafy development. In the truly leafy Liverworts there is a ventral row of leaves, and a row of lateral leaves on either side. These leaves are more or less clearly two-lobed, and the lobes are often unequal (Fig. 310, *A*). Sometimes a lobe may become highly specialised, as in *Frullania* (Fig. 310, *B*), where that which is downward-directed develops as a water-sac, or pitcher, effective in collecting and holding water in this epiphytic or rock-dwelling genus. On the other hand, in *Trichocolea* the leaves may be divided into narrow laciniae, which collectively hold water as in a sponge. Thus it appears that there is a wide scale of adaptation

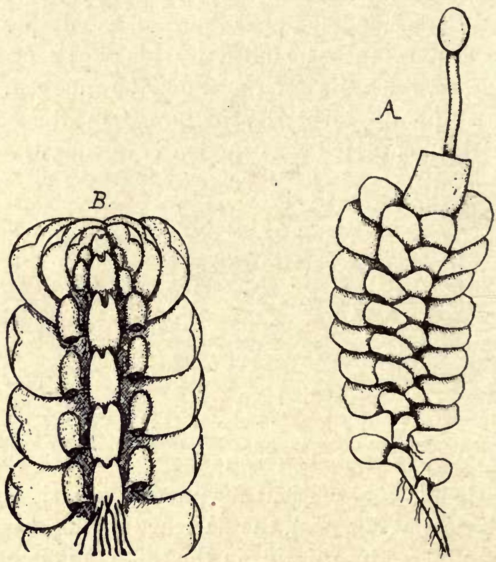


FIG. 310.

***A*, *Scapania nemorosa*,** dorsal view of the leafy shoot, which bears a sporogonium at its tip. ***B*, *Frullania tamarisci*,** view of leafy shoot from below, to show the ventral row of leaves, and the two lateral rows, of which the lower lobes form pitchers. *A* has the "succubous," *B* the "incubous" disposition of the leaves. (After Cavers.)

of the gametophyte in Liverworts. Its results offer analogies with the special adaptations seen in the sporophyte of Flowering Plants.

The sexual organs are essentially similar to those of the Mosses; but there are differences in their segmentation. This suggests that their origin may have been distinct. In the thalloid Liverworts they are always borne on the morphologically upper surface; but by various means they are carefully protected, being sometimes sunk deeply in the thallus (Fig. 311). In the Jungermanniae they are covered in by envelopes, the number and variety of which give useful features in classification. A particular interest attaches to those which develop a "marsupium," that is a nursing-sac surrounding the archegonia, and penetrating deeply into the soil. Such arrangements, both in the vegetative structure of the gametophyte and in the disposal and protection of the sexual organs, suggest that the Liverworts are making the best of subaerial life, to which their simple structure is not in itself well suited. Their fertilisation is by movement of spermatozoids motile through water.

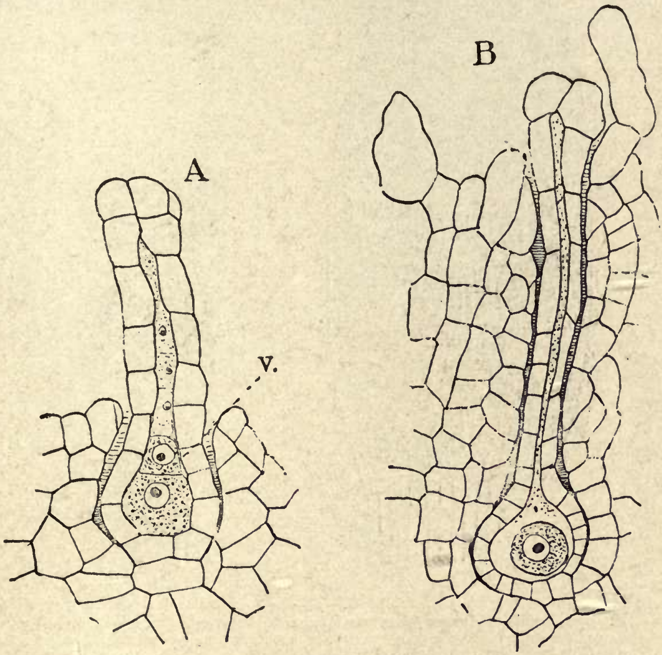


FIG. 311.
A = archegonium of *Riccia trichocarpa*, showing ventral canal cell (*v*) and ovum. (× 525).
B = ripe archegonium of *Riccia glauca*. (× 260). (After Campbell.)

The sporogonium itself is on a simpler scale than that of the Mosses. Excepting the peculiar group of the Anthoceroteae, it does not carry on photo-synthesis, nor is there any complete columella. Moreover the sporogonium is longer enclosed in the archegonial wall; but it bursts it at maturity, when the seta elongates, bearing outwards the spherical head. There is no operculum, but the relatively thin wall bursts, usually into four valves, and the spores, interspersed among fibrous elaters that help to distribute them, are exposed as a flocculent mass to the breeze, and are scattered in the dry state. Though the details are different from those of the Mosses, the end is the same (Fig. 312).

On the other hand, certain Liverworts have very simple sporogonia. This is conspicuously the case in the *Ricciaceae* (Fig. 313), where it is spherical, with no distinction of apex and base, and no elaters. The sporogonial wall is one layer thick, and is disorganised at ripeness.

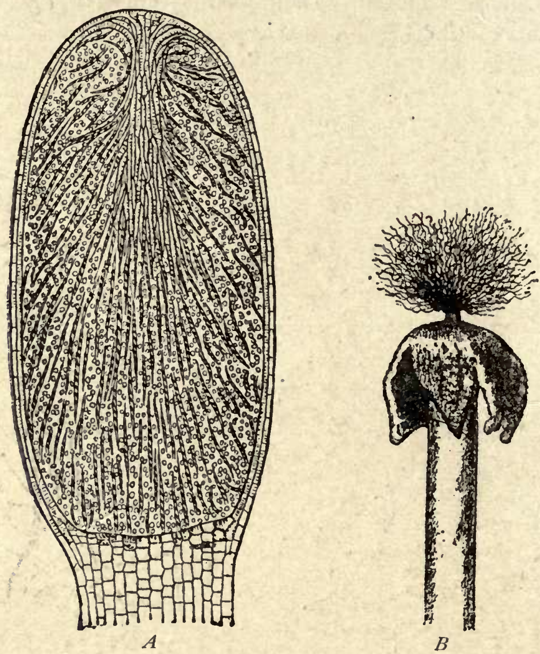


FIG. 312.

A, Ripe capsule of ***Aneura pinguis*** in longitudinal section. From the summit an elaterophore hangs into the spore-cavity, in which are many spores and detached elaters. Magnified. (After Goebel.)

B, Capsule of ***Pellia calycina***, burst, and emptied, showing the valves of the wall recurved, and an elaterophore rising from the base, bearing many threads. (After Goebel.)

The spores are scattered on decay of the thallus. This is the simplest condition of the sporophyte known in Archegoniate Plants. It is a familiar subject of comparative discussion whether the simplicity that *Riccia* shows is really primitive or the result of reduction from some more complex type.

Comparing such facts from the Bryophyta with those relating to the Pteridophyta, it is apparent that both are "amphibians," in the sense that they cannot complete their life-cycle without the presence of external fluid water. This tends to restrict them to moist situations, where their sexual propagation by motile spermatozoids can be carried out. In any organism with a life-cycle punctuated by the two stages of the spore and the zygote, there are two possibilities of somatic expansion, viz. in the diploid sporophyte and in the haploid gametophyte. In the Bryophytes the second alternative has been fully exploited. Their characters depend upon the development of the gametophyte to the highest condition in which it is seen in Land Vegetation. The details of this development run parallel with those of the sporophyte in Vascular Plants, so that the two present a series of analogies. The

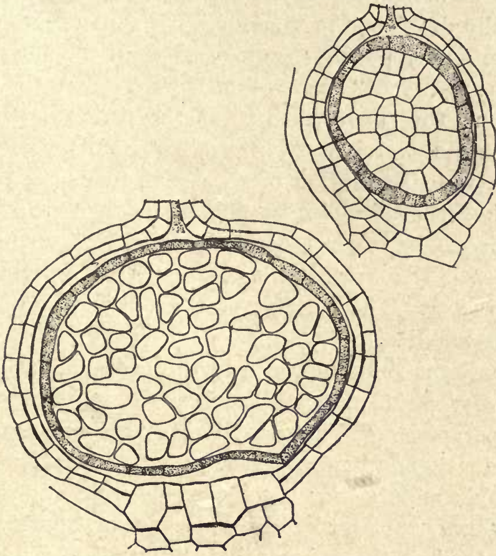


FIG. 313.

Ricciocarpus natans. Young sporogonia still surrounded by the archegonial wall. The younger (× 666) shows the wall of the sporogonium shaded, surrounding the sporogenous cells. In the older (× 560), these are separated as the free spore-mother-cells. (After Garber.)

most striking are seen in the organs of photo-synthesis, in the conducting tracts, and in the grouping of the organs of sex. In the sporophyte of Vascular Plants the typical photo-synthetic organ is the leaf-blade, with its ventilated mesophyll and stomatal control. In the gametophyte of Mosses and Liverworts a similarly ventilated structure is seen in the leaves of some of the larger Mosses (Fig. 300), and in the thallus-structure of the Marchantiales (Fig. 309). These are, however, parts of the gametophyte, and the ventilated structure is here produced mainly by involution of the outer surface, while in Vascular Plants it arises from intercellular splitting of the cell-walls. The physiological end is the same in both cases, but the place and the means are different. Plainly these are the results of parallel evolution, or homoplasy.

So also the conducting tissues seen in the stem of large Mosses, such as *Polytrichum*, show in their connections with the leaves, as well as in their construction of hydrom and leptom, similarities with the conducting system of Vascular Plants (Fig. 299). But again the comparison is between the gametophyte on the one hand and the sporophyte on the other; while the isolation of such phenomena in the larger Mosses indicates that the conducting tissues are an adaptive feature specially developed in them, and not general for all Mosses.

There is also a very peculiar analogy between the flowers of Angiosperms and the so-called "flowers" of Mosses, where the perichaetial leaves surround the sexual organs, as the perianth surrounds the androecium and gynoecium in Flowering Plants. There is even parallelism in the distribution of the sexes, for such "flowers" in Mosses may be hermaphrodite or unisexual. Notwithstanding this likeness it is necessary to keep clearly in mind that such comparisons deal with essentially different things, though both involve the sex-distinction (p. 360). The interest of them lies in the fact that the similarity exists at all.

Such comparisons show how nearly the evolution of the gametophyte in the Bryophyta may follow along the same lines of adaptation as the sporophyte of Vascular Plants. The end is the same for both, viz. to develop on land as large a vegetative system as possible, so as to provide material for the largest possible number of germs. The one phylum has solved it by enlargement of the sporophyte, which thus becomes the substantive "Plant" of Vascular types. The other has solved it by elaboration of the gametophyte, which has similarly become the substantive "Plant" of the Bryophytes. Both have one foot in water and the other on land. In Vascular Plants it is the sporophyte foot that is more firmly set on land. In the Bryophytes it is the gametophyte foot that is more securely placed, and the sporophyte is dependent upon it, not temporarily, but up to the time of maturity of its spores.

DIVISION V.

THALLOPHYTA.

CHAPTER XXIII.

THALLOPHYTA.

INTRODUCTORY.

THE Seed-Plants and the Archegoniatae constitute by far the greater part of the Flora of the Land. But when these are put on one side, there still remains a residuum of organisms properly ranked as Plants, very numerous, though often individually small and inconspicuous, and many of them dwellers in water. They are collectively designated the "THALLOPHYTA," or thalloid plants, since a general feature in them is the absence of that differentiation of the shoot into axis and leaf which is characteristic of the higher forms. It must not be assumed that all the organisms thus grouped under a common designation are necessarily akin to one another. They are found to be naturally separable into distinct groups or *phyla*. The plants belonging to these phyla may be so arranged as to show progress from simpler to more complex forms. Such sequences probably represent with some degree of accuracy *lines of descent*. Commonly the simpler terms of these distinct phyla are more alike than the more advanced. Thus the lines of descent are *divergent*, and the Thallophytes would appear to represent a brush of phyletic lines radiating outwards from some simpler source.

Though none of the Thallophyta have themselves achieved that highest development seen in Land-Vegetation, many have advanced far in their evolution. In mere size the Brown Seaweeds include the gigantic Tangles, which are among the largest of living organisms. In complexity of propagative method no group of Plants shows more intricacy than the Red Seaweeds.

In physiological resource the Fungi are the most diverse. But each of these includes simple types, which link up more easily with other organisms than do the extremes. Each phylum has worked out its own divergent line of advance independently of the rest. Some degree of parallelism in the progressions may then be anticipated, and is actually found to exist.

The readiest basis of distinction of these natural groups of Thallophyta is by colour. The most important cleavage is according to the presence or absence of chlorophyll, or of some of its derivatives. This separates the FUNGI, which have no chlorophyll or kindred colouring matters, from the ALGAE, which have. The Algae again fall into distinct groups on the basis of colour-difference. Those which have full green chlorophyll, such as is seen in Land-Vegetation, are designated the *Chlorophyceae*. Others are characterised by their olive green or brown colour, which is due to the presence of a brown colouring matter (phycophaein) in addition to the chlorophyll. It is characteristic of the Brown Tangles, or *Phaeophyceae*. A third series have a prevalent red pigment (phycoerythrin) in addition to their chlorophyll, and they are called the *Rhodophyceae*, or Red Seaweeds. These colour-distinctions are not absolutely constant. But it happens that the colours mentioned run closely parallel with other characteristics of form and propagative method, by which these large groups are more strictly defined, so that it becomes a true indication of their distinctness.

The colourings have a physiological meaning. The absence of chlorophyll indicates dependent nutrition, as in the Fungi. It may be objected that, while the Thallophytes are classified by colour, in Flowering Plants such differences were not taken into account in their classification. But in dealing with Organic Nature, which has progressed along individual lines, consistency of method in classification is not possible, if the grouping is to follow the course which evolution has actually taken. The reason why the method adopted for Flowering Plants will not apply for the Thallophytes is that in the former the change to irregular nutrition happened late. They are plainly Flowering Plants that have changed their mode of nutrition. But in the case of the Fungi we are dealing with a very ancient change. Fungi existed in the Palaeozoic Period. Thus their irregular nutrition will have influenced their development from very early times.

The colours distinctive of the three groups of Algae are related to photosynthesis. A brown or red tint makes self-nutrition possible deep down in sea-water. Speaking generally, the Red Seaweeds are prevalent at the lower levels, while the Browns extend from the highest levels downwards, but stop short of the greater depths. The Greens are more widely diffused, but they occur mostly at the higher levels, and they are the prevalent Algae of fresh water.

If we accept this general view of the Thallophytes, it becomes a question whether there is any living group of organisms which represents approximately the source from which they may have originated. It is a very general opinion that such a source is to be found among the Flagellatae, a family which it is difficult to refer definitely either to the Kingdom of Animals or of Plants. It includes many of those organisms which cause certain diseases in man and other animals, and these are more definitely animal in their characters. But others, such as *Euglena*, possess

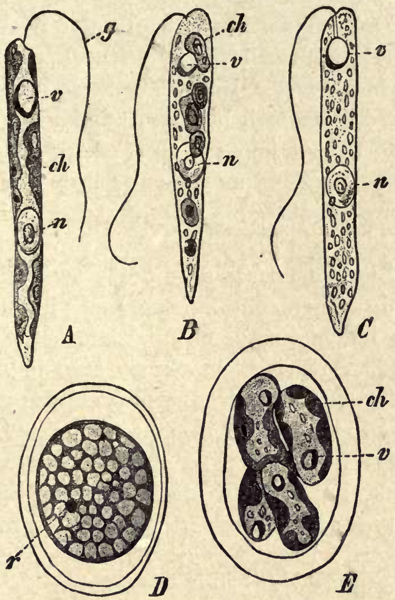


FIG. 314.

Euglena gracilis. *A*, Form with green chromatophores (*ch*); *n*=nucleus; *v*=vacuole and red eye-spot; *g*=flagellum. *B*=hemi-saprophytic form with small green chromatophores. *C*=colourless saprophytic form occurring in nutrient solutions, in absence of light. *D*=resting cyst of the form *C*: *r*=red eye-spot. *E*=germination of the resting cyst of the form *A*, by division into four daughter cells, which later escape. (After Zumstein.) (*A*, *C* × 630; *B* × 650; *D*, *E* × 1000.) (From Strasburger.)

features characteristic rather of Plants. *Euglena* is found commonly in summer, colouring the foul water that drains from manure heaps a bright green. The organism is then seen in the motile state, as a free-swimming, naked protoplast of elongated form, towed along by a single flagellum (Fig. 314). There is a central nucleus (*n*), several green-coloured chromatophores which vary according to the conditions (*ch*), a contractile vacuole (*v.*) communicating by an oesophagus or funnel with the exterior, and a red eye-spot, or stigma, lying at the junction of oesophagus and vacuole. The base of the flagellum passes through the oesophagus, and is attached by a branched base to the inner surface of the vacuole. In this state *Euglena* can feed itself by photo-synthesis, but it probably obtains simultaneously some degree of saprophytic supply from the foul water in which it lives. When well nourished it may contain large paramylum bodies, but not starch. It multiplies by fission, the nucleus dividing first (Fig. 315). When starved for a lengthened period an encysted form is assumed. The chromatophores diminish in size and colour, and storage materials appear in the contracted protoplasm, which is then surrounded by a thick wall (Fig. 314, *D*). In this state it can resist conditions that are adverse. But when these are favourable again the cyst germinates; its wall becomes mucilaginous; the contents usually divide into two or four (*E. gracilis*), or even more parts (*E. viridis*), which, after showing movement within the wall, are finally set free as naked protoplasts (*E*). No sexual process has been observed in *Euglena*, though certain Flagellates show conjugation.

The common *Euglena viridis* does not grow well in spring water, but it flourishes in water containing organic impurities. Probably photo-synthesis is its chief mode of nutrition, but it can also act as a partial saprophyte. This is more clearly seen in *E. gracilis*, which has been shown to be either autotrophic or purely saprophytic according to circumstances. Fig. 314, *C*, shows the colourless form grown in the dark in a nutritive medium. The chromatophores are reduced to small pale plastids, but still the organism appears well nourished. This saprophytic type can then be restored to the autotrophic condition by exposure to light. It thus appears that certain Flagellates may temporarily or permanently make use of a saprophytic mode of nutrition.

Organisms which show characters so versatile suggest several distinct lines along which evolution is possible; and those lines if realised would give rise to features characteristic of the largest groups of living beings. The motile green condition, with the capacity for photo-synthesis, if it becomes encysted, loses its motility while it achieves protection. The encysted form of *Euglena* after division of its protoplast is so like certain Algae allied to *Palmella* that it has been called the "*Palmella-state*." The resulting cells remain grouped for a time. If that state become permanent, and the divisions numerous, a cell-colony would be formed of a type characteristic for Plants. But the protoplasts of *Euglena* may soon escape and become motile again, a condition which is seen repeated commonly in the propagative cells of Plants up to the Gymnosperms. *Thus the* *encysted state of Euglena suggests a possible mode of initiation of the encysted construction characteristic of Plant-Forms* (compare Chapter IX.).

The saprophytic mode of life in *Euglena*—or parasitic, as it is in many other Flagellates, which are then independent of light and chlorophyll—suggests a distinctively animal existence. Here motility is retained, and encystment appears only as an occasional incident. This behaviour of *Euglena*, an organism in which sexuality does not exist, or at least has not been observed, indicates that the segregation of Animals and Plants may have antedated sexuality. But such ideas must not be taken for more than they are worth, since they raise questions which cannot be definitely answered. Nevertheless they

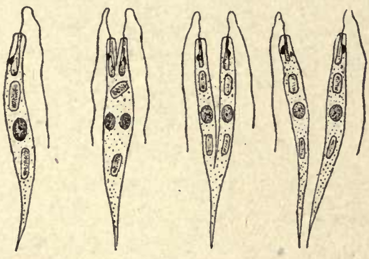


FIG. 315.
Successive stages of fission of *Euglena*: semi-diagrammatic.

are worthy of consideration as giving a point of view which will have its value in directing the study of the lower organisms, whether of the Animal or of the Vegetable Kingdoms.

The instability of nutritional method in *Euglena*—and especially its mixed nutrition, partly photo-synthetic and partly saprophytic, as it grows strongly in foul water—finds its parallel in the mixed nutrition of many land-living Plants. It seems probable that irregular nutrition has been widespread, from very low forms such as *Euglena* to the highest Flowering Plants. At various points in the series the dependence upon physiological supply other than by photo-synthesis may have been accentuated. The parasitic Seed-Plants, such as *Viscum* or *Cuscuta*, and the saprophytes, such as *Neottia* or *Monotropa*, are cases where it was adopted relatively late, in forms with their character already stamped as Seed-Plants. The various groups of Fungi are cases where the physiological dependence was established early, but after the encysted state had been definitely adopted. A similar segregation, but earlier still, with absence of encystment, would account for the establishment of the Animal Kingdom.

Such suggestions as these are based upon the actual facts observed in simple organisms referable to the Flagellatae. It may be uncertain whether or no these forms were or were not like the original sources from which Vegetable and Animal Life sprang. They serve however, to give some idea of the possible origin and early relations of the larger groups of living organisms, and of their differentiation on the basis of nutrition, and of certain fundamental features of their structure. In point of habitat the significance of these comparisons cannot be mistaken ; for all these organisms are either aquatic, or at least they live where water is readily available.

CHAPTER XXIV.

BROWN ALGAE (*PHAEOPHYCEAE*)

The Brown Algae, or *Phaeophyceae*, include a large proportion of the Seaweeds commonly found between the tide-marks, and extending downwards to greater depths. Some of them are delicate filamentous growths, branched or unbranched (Ectocarpeae). Others are larger and more complicated in structure, with ribbon-shaped thallus (*Dictyota*). Some, of leathery texture, attain gigantic dimensions, the Tangles of the colder oceans being among the largest of living beings (*Laminaria*, *Nereocystis*, *Macrocystis*). The most familiar are the species of *Fucus* found on all British coasts, of which *F. vesiculosus* is the Common Bladder Wrack. The smaller forms show gradual steps of increasing complexity, from the simple septate unbranched filament, through various modes of branching and cortication, to the massive tissue-formation seen in the larger Tangles.

The thallus of the larger forms is usually flattened, and bilaterally symmetrical (p. 172). It shows forked branching, often very perfectly dichotomous, and in a single plane. The result is that the whole frond is fan-shaped, as is seen particularly well in the native species *Fucus serratus* (Fig. 316). The thallus is attached by a holdfast to some firm body such as a rock; but the gulfweed (*Sargassum bacciferum*) is exceptional in floating freely. The holdfast applies itself so closely to the irregularities of the surface that the stalk will often break before it would come away. In *Fucus* the holdfast is discoid, in *Laminaria* and others it may be branched and root-like. But its function is only mechanical, not absorbent. The thickness of the stalk which arises from it is proportional to the size of the thallus it has to moor. A plant so constructed is well fitted to resist the swirl of the waves, keeping its hold, and though pliant, retaining the form of its leathery frond. If exposed between tide-marks it lies down flat, and where the growth is dense the plants mutually protect one another from drying.

There is in many of these seaweeds a localised apical growth with an apical cell. In *Fucus* the growing point lies in a depression at the extreme tip. In others (*Dictyota*, *Sphacelaria*) the apex projects. The

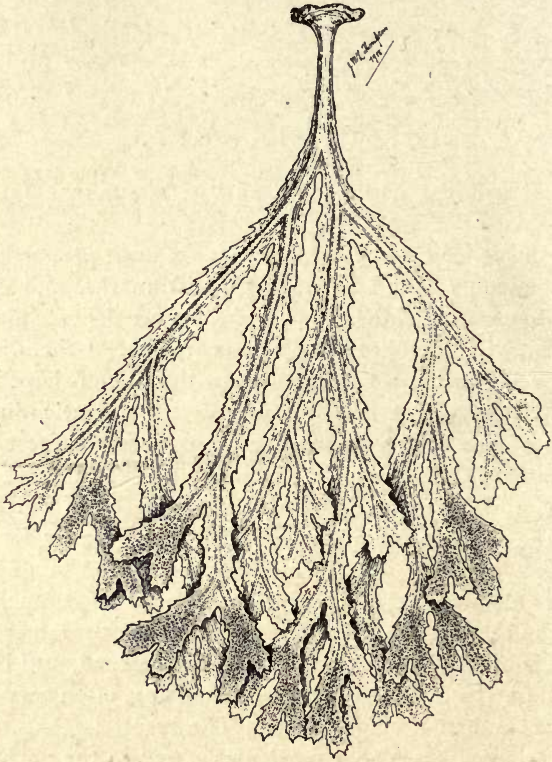


FIG. 316.
Drawing of an actual plant of *Fucus serratus*. (½ Nat. size.)

segmentation of the apical cell is often very regular, the form and succession of the segments varying in accordance with the form of the tip itself. In other cases intercalary growth is dominant. This is seen in the simple filaments of the Ectocarpeae, and in the more complex thallus of *Cutleria*. But it is shown on the large scale in *Laminaria*, where a new frond is formed each season between the old one, which is thrown off, and the persistent stalk (Fig. 317).

In simple forms the cells are all alike. Soft cell-walls surround a uni-nucleate protoplast, which includes simple brown chromatophores.

The product of photo-synthesis appears as semifluid grains of a carbohydrate, "fucosan," in place of starch. In the larger forms the tissues are differentiated. For instance, in *Fucus* the cells of the superficial layer are thin-walled, and divide actively; they are covered externally by a layer corresponding to cuticle. They are the chief seat of photo-synthesis, and of tissue-formation (Fig. 318). Passing inwards from this layer the mucilaginous cell-walls become more and more swollen, so that the deeper-seated tissues of an old thallus consist of a bulky mucous matrix, in which the cells themselves appear as a complicated network (Fig. 319). Centrally there is a firmer conducting cord, which is well defined in old stalks of the larger Tangles. It contains many tubes with sieve-structure and callus, closely comparable to the sieve-tubes of Vascular Plants, and serving like them for transport. In large stalks an ill-defined cambial activity provides for thickening and increased mechanical strength. This is still further secured by "intrusive hyphae," which burrow through the softer tissues, and brace them together. In this way they acquire their tough and resistant but yet pliant character. We thus see that both in external form and internal structure the Brown Seaweeds cover a wide range, from the simple to the complex.

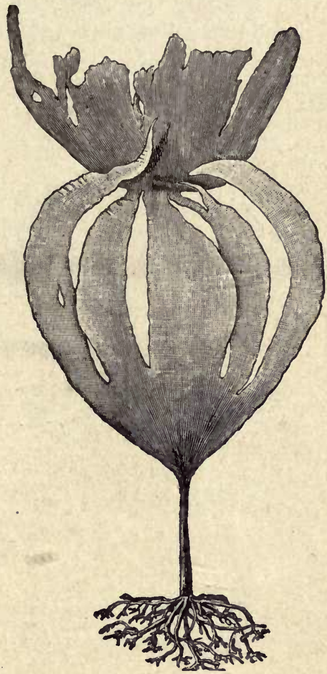


FIG. 317.
Laminaria, thallus showing a new frond, intercalated between the stalk and the old frond, which is being thrown off. (Reduced.) (After Strasburger.)

In their sexual propagation they also show an advance, which runs in some degree parallel with their structural progress. Successive steps in differentiation of the sexes may be found. The simplest forms produce *isogametes* which are *motile*. More complex forms show differentiation of sexes, the small *spermatozoids* being *motile*, but the larger *ova* are *non-motile* primordial cells. The Phaeophyceae are thus divided into two orders: the *Phaeosporeae*, where both gametes are motile, and the *Cyclosporeae*, where only the spermatozoids are motile. To the first belong the Ectocarpeae, Laminarieae, and

Cutlerieae, to the latter the Dictyotaceae and Fucaceae. Examples selected from these illustrate probable steps in sexual differentiation.

The propagative cell of the Brown Seaweeds is very constant in its form. It is actively motile in the water into which it is set free. It is a pear-shaped, nucleated protoplast, with two cilia attached laterally so that one is directed forwards the other backwards. They are inserted close to a red eye-spot, which as a rule is closely related to a yellow chromatophore (Figs. 320, *B*; 324, 3). The constancy of this type shows the probable phyletic unity of the Brown Algae.

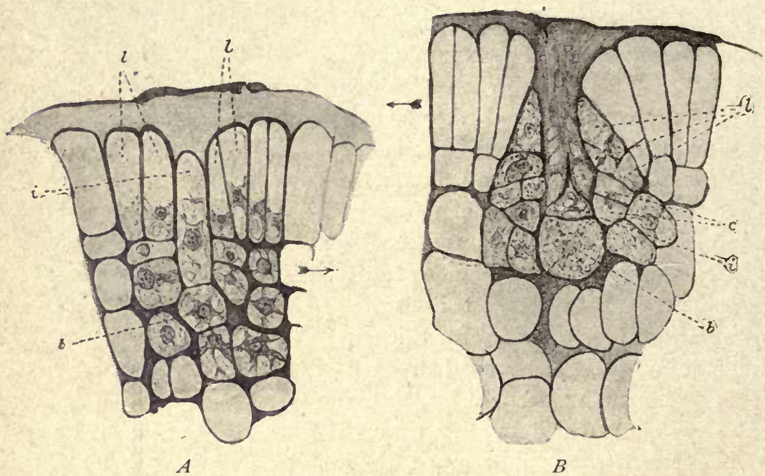


FIG. 318.

A, *B*, successive stages in origin of a conceptacle of *Fucus*. Incidentally they show the active division of the cells of the superficial layer (*l*, *l*) and its production of internal tissues. (× 530.) F. O. B.

In the simpler types propagation may be either vegetative, carried out by *zoospores* produced in *unilocular sporangia* (Fig. 320, *A*); or sexual, carried out by *gametes*, produced in *plurilocular sporangia* (Fig. 323). In form and motility the zoospores and gametes are alike; but the former are larger and germinate directly into new plants without conjugation, while the latter are smaller, and conjugate before germination. It seems probable, therefore, that the gamete is really a zoospore specialised for conjugation.

In *Ectocarpus siliculosus* all the gametes appear alike, but they are distinguished as male and female by their behaviour. These are produced from distinct sporangia, which may be borne on the same or on different plants. Those gametes which are functionally female and receptive soon lose their motility, becoming fixed to a substratum by the forward cilium. Such fixed females become centres of attraction for the still motile males, which collect round them in number, and come into contact with the female by their forward cilium (Fig. 321, 1). Presently one of them draws up to the female and begins to fuse with it (2); all the rest at once move away. Gradually the fusion is completed (3-5), the resulting zygote rounds off and

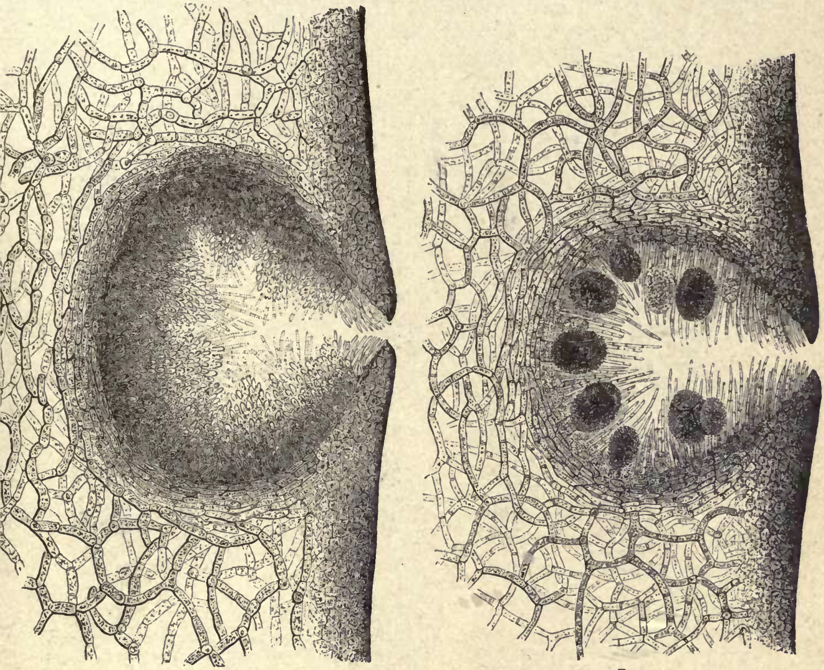


FIG. 319.
A, Mature male conceptacle of *Fucus serratus*, filled with branched antheridial hairs. (After Thuret.) *B*, Mature female conceptacle of *Fucus serratus*, containing unbranched hairs, and oogonia. (After Thuret.) Incidentally these drawings show the structure of the mature thallus (p. 379).

forms a cell-wall, and may presently germinate into a new plant. In *E. siliculosus* both types of sporangia and of gametes are alike in form. But in *E. secundus* the sporangia (*gametangia*) are not alike; and they produce gametes of different sizes (Fig. 322, i.). The smaller-celled gametangia (*antheridia*) produce smaller gametes that are male (*spermatozoids*, ii.); the larger-celled (*oogonia*) produce larger gametes that are female (*ova*, iii.). But still they are of the same form as the zoospores of the whole group. After their escape the ova soon lose their motility, and their fertilisation by the smaller spermatozoids is as in *E. siliculosus* (iv.-vi.). A third example is seen in *Cutleria*, in which the male and female gametangia, as well as the gametes which they produce, differ still more markedly in size (Fig. 323). These steps in sexual differentiation make the condition seen in *Fucus* intelligible.

In the Fucaceae there are no means of vegetative propagation, the increase in numbers being wholly by the sexual process. The sexual organs are not exposed, as in the simpler Algae, but borne

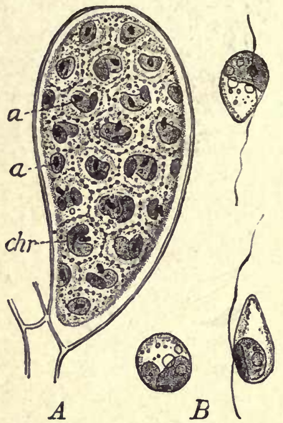


FIG. 320.

A, Pleurocladia lacustris. Unilocular sporangium with its contents divided up into zoospores. *a*=eyespot. *chr*=chromatophore. (After Klebahn.) *B*=*Chorda filum*, zoospores. (After Reinke.) (From Oltmanns' *Algae*.)

FIG. 321.

Ectocarpus siliculosus. 1, female gamete surrounded by a number of male gametes. 2-5, stages in the fusion of gametes. 6, zygote after 24 hours. 7-9, fusion of the nuclei as seen in fixed and stained material. (1-5 after Berthold; 6-9 after Oltmanns.) (From Strasburger.)

in *conceptacles*, which are cavities hollowed out of the thallus, and clustered at the ends of its branches, thickened to accommodate them (Fig. 319). Similar conceptacles bearing tufts of hairs but no sexual organs are scattered more or less sparsely over the vegetative thallus. In *Fucus serratus* the male and female organs are borne on distinct plants, but in many species they may appear in the same conceptacles. A median section through a male conceptacle shows how the flask-shaped cavity opens to the outside by a narrow pore, and is at maturity filled by richly branched hairs, which arise from the tissues bounding the conceptacle, and bear the numerous minute *antheridia* (Fig. 319, *A*). The female conceptacle is of like structure, but bears unbranched hairs, and associated with them are the large

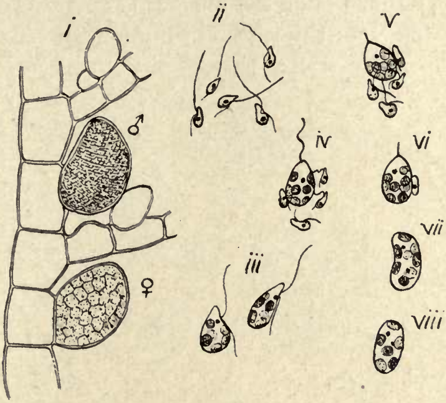


FIG. 322.

Ectocarpus secunda. (After Sauvagean.) i. filament bearing plurilocular sporangia (or gametangia): ♂ male, ♀ female. ii. male gametes. iii. female gametes. iv.-vi. stages in fertilisation. vii., viii. zygotes. (i. × 200; ii.-viii. × 500.)

oogonia, which are large enough when mature to be seen with the naked eye (Fig. 319, *B*).

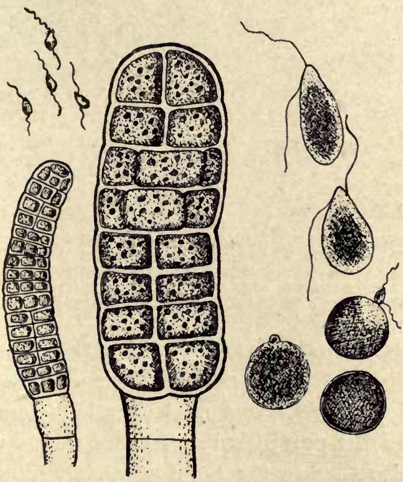


FIG. 323.

Cutleria multifida, showing the smaller, male gametangia (or plurilocular sporangia), and the larger female. Top-left are spermatozoids, top-right are ova. Below are three stages of fertilisation. (× 500.) (After Reinke.)

The antheridium itself is an oval unicellular body, surrounded by a cell-wall. When young it contains a single nucleus, which divides to form 64 nuclei, each of which becomes the centre of a spermatozoid. The cytoplasm divides into as many portions, and each is found to contain a red eye-spot beside the nucleus (Fig. 324, 2). The contents slip out when ripe from the ruptured outer wall, as a mass still surrounded by the inner wall: this soon deliquesces, and sets them

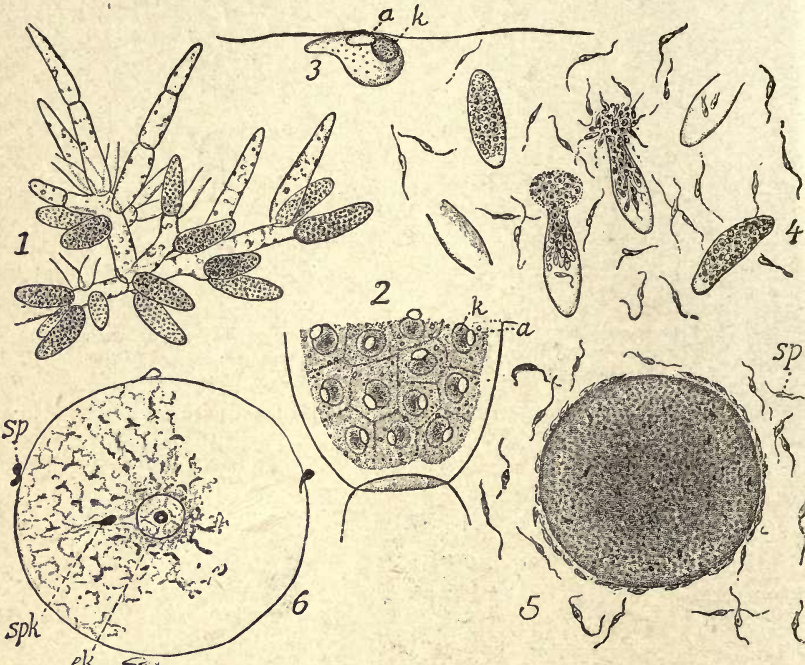


FIG. 324.

Fucus. 1, group of antheridia. 2, part of an antheridium showing developed spermatozoids. 3, spermatozoid; *a*=eye-spot; *k*=nucleus. 4, Isolated antheridia liberating spermatozoids. 5, ovum surrounded by spermatozoids. 6, section through a fertilised egg; *ek*=nucleus of egg; *spk*=nucleus of sperm; *sp*=spermatozoids: (1, 4, 5 after Thuret; 2, 3 after Guignard; 6 after Farmer.) (From Strasburger.)

free as 64 *motile spermatozoids*, each with the characters usual for the Brown Seaweeds (4). The oogonia though larger are of the same pattern. Each has at first one nucleus; but here it divides only to form eight, and the cytoplasm undergoes cleavage into *eight large ova*. They are also shed in the same way, and round themselves off as non-motile eggs (5).

A comparison of the antheridium with the oogonium in the Fucaceae shows that they are probably results of differentiation from a common source. When an oogonium is to be formed, a cell of the wall of the conceptacle grows inwards into the cavity, and divides to form a stalk-cell and an oogonium (Fig. 325, A, B, *st.*). In *Sarcophycus*, however, the stalk is branched, and a succession of oogonia may be produced, as is seen in the antheridia of *Fucus*. The antheridial hair of *Fucus* may start precisely in the same way as the oogonium, the terminal cell forming the antheridium. But the growth does not stop there: the stalk-cell shoots out laterally and produces another antheridium, and the process may be continued with irregular sympodial repetition (Fig. 324, I.). This finds its biological explanation in the need for continued supply of numerous spermatozoids, so as to secure fertilisation over a prolonged period. The large number is further ensured by the divisions in each cell being continued to 64.

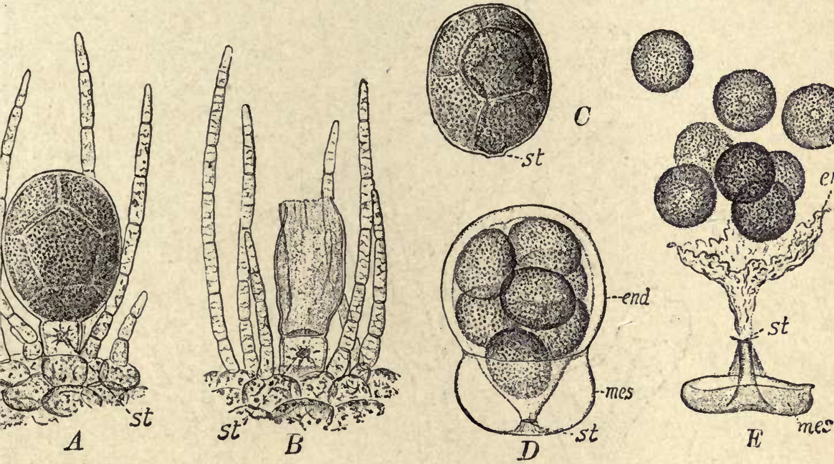


FIG. 325.
Fucus. *A*, oogonium, the contents of which have divided into eight eggs. *B*= oogonium, from which the contents (*C*) have been extruded. *D*, *E*, liberation of the eight eggs; *st*=stalk; *mes*=middle—*end*=inner layers of the oogonial wall. (After Thuret.) (From Strasburger.)

The solitary oogonia, with their few ova, find their biological elucidation in the facts that the ova are large, and have a strong chemotactic influence on the motile spermatozoids. Their size gives a high degree of certainty of successful germination if once fertilised. Their attractive influence secures a high probability of fertilisation, notwithstanding their immobility, which has followed on increase in size. But *Fucus* is not the last term of the series of reduction of the oogonium. In *Ascophyllum* only four ova are matured in each, in *Pelvetia* two, and in *Himanthalia* and others only one. Vestigia of the atrophied eggs are found, which clearly indicate that their number has been reduced. Thus the Brown Algae form a coherent series of sexual differentiation. Their sexual cells probably originated from motile zoospores, all alike. The first functional though not formal distinction of sex is seen in *Ectocarpus siliculosus* (Fig. 321), and confirmed by difference of size of the gametes in *E. secundus* (Fig. 322). Steps in loss of motility are seen in these plants, and in *Cutleria* (Fig. 323), while in *Fucus* the large ovum is entirely non-motile (Fig. 325). Finally, in *Himanthaila* it occupies the whole oogonium:

its large size giving such security of germination as to justify the reduction in number to one.

In Fucoids which live submerged the gametes may be set free at any time. But when exposed between tide-marks it will be chiefly on the rising tide that they are liberated. Exposed to the air the mucous thallus shrinks on drying, and the pressure of the contracting tissue may be seen to squeeze out the ripe antheridia and oogonia,

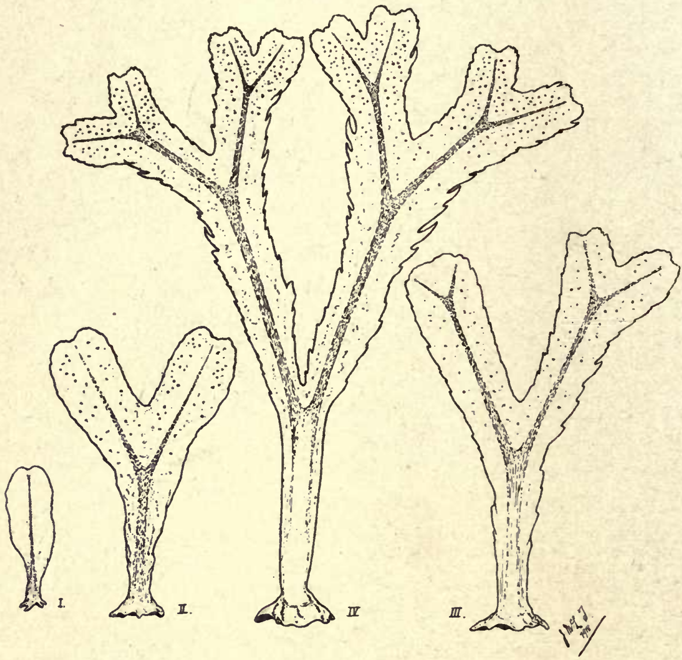


FIG. 326.
I.-IV. Drawings direct from successively older Plants of *Fucus serratus*, showing the regular dichotomy.

which may be recognised by their yellow or olive colour, through the open pores of the conceptacles. If these be collected fresh in separate watch-glasses in sea water, the final liberation of the minute motile spermatozoids (Fig. 324, 4) and of the much larger non-motile eggs (Fig. 325, *E*) can be easily followed. If then a drop of water containing the former be added to a drop containing ova on a slide, many spermatozoids will be seen to collect round each ovum, which thus shows its attractive influence on their movements (Fig. 324, 5). But only one penetrates each egg, and its nucleus has been followed on its course through the cytoplasm till it fuses with the nucleus of the ovum (Fig. 324, 6). The rest at once move away, as though a repellent influence from the egg had replaced the previous attraction.

The immediate consequence of fertilisation is the deposit of a cell-wall covering the zygote. It settles on some solid substratum, and germinates directly into a new *Fucus* plant. Stones on a rocky shore where Fucoids grow may be found in summer covered by a dense growth of myriads of these young plants (Fig. 326).

In the life-history of *Fucus* the increase in numbers is exclusively through the sexual process. There is no production of spores, nor any non-sexual propagation, as there is in the simpler Brown Seaweeds. But in *Dictyota*, which is grouped with the Fucaceae in the Cyclosporeae, there is an alternative production of tetraspores. Separate plants in *Dictyota dichotoma* bear respectively tetraspores, oogonia, and antheridia. The nuclei in the first of these plants are diploid, with 32 chromosomes. The nuclei of the male and female plants are haploid, with only 16 chromosomes. Reduction takes place when the tetraspores are formed, and these on germination give the sexual plant. The analogy of the tetraspores with the spore-tetrad in Land Plants is obvious. But here the haploid gametophyte and the diploid sporophyte are alike in form. In *Fucus* reduction takes place in the first divisions respectively of the antheridial and oogonial cells. The whole plant is a diploid sporophyte, arising from the germination of the diploid zygote. Such facts raise questions as to the origin of the alternate generations seen in *Dictyota*, or their absence in *Fucus*. But these can only receive their final answer after exhaustive examination of the nuclear cycle in the simpler members of the series. In them the details are still unknown.

It seems clear from the peculiarity and the constancy of form of their propagative cells that the Brown Seaweeds are a naturally related group of organisms. They illustrate steps of advance in respect of form, structure, and propagative method; and these follow for the most part along parallel lines. Accordingly they may be held to represent a progressive series. That they are ranked as Thallophytes is no sufficient reason for holding them all as primitive. Their higher terms show high structural adaptation to their requirements, and they are in their own habitat eminently successful plants. They may therefore be held as the ultimate exponents of an evolution limited by its surroundings, and distinct from other lines of Descent.

RED ALGAE (*RHODOPHYCEAE*).

The Red Algae (*Rhodophyceae*) are a separate group, distinguished by their method of propagation from all others. They are mostly marine, spreading from the zone between tide-marks to deeper levels, and finding their limit at about 150 feet below low-water mark. Their colour varies from pink to purple, or reddish brown. This is due to chromatophores containing red pigment which masks the chlorophyll. The colouring has its relation to light. The greatest activity of photo-synthesis is in light complementary to the colour of the plant. Ordinary plants make special use of the rays at the red end of the spectrum; but for Red Algae rays further along the spectrum are effective, and it is the rays towards the blue end of the spectrum which penetrate into the depths of sea water. But all of the *Rhodophyceae* are not red. It is significant that *Lemanea*, which is exposed to ordinary sunlight in shallow fresh-water streams, is green.

FIG. 327.
Nemalion multifidum. 1, Branch bearing antheridia to the left and a carpogonium to the right, with spermatia, some of which adhere to the trichogyne. 2-5 are successive stages of development of the very simple fruit. (After Kny.)

In form the Red Algae are various, but never large. They include plants which in form and colour are among the most beautiful, and therefore are prized by collectors. They may consist merely of branched septate filaments: or fronds, variously thickened and flattened, may be formed by matting and webbing of many filaments together. Often they are fan-shaped and sometimes lime-encrusted. The feature they have in common is their method of sexuality. The male organs are unicellular, the whole content of each cell escaping as a naked, *non-motile spermatium* (Fig. 327, 1). The female organ is a *carpogonium*, consisting of a cell with an enlarged base, and elongated upwards into a filamentous *trichogyne*. This receives the non-motile spermatium, and then shrivels: the *carpospores* arise directly or indirectly from the enlarged base. *Fertilisation is indirect*, in the sense that the nucleus of the spermatium received by the trichogyne is passed down to the base, where fusion and spore-formation follow (Fig. 327). This is the leading character of the Red Algae, and it is worked out in some of them with extreme complication of detail in the method of transfer of the nucleus.

In some Red Algae, such as *Nemalion*, which is one of the simplest of them all, no other organs of propagation are known. But in most of them *tetraspores* are found, in the production of which reduction of chromosomes has been demonstrated. The nuclear cycle has been fully worked out in *Polysiphonia violacea*, in which the tetraspores and sexual organs are borne on separate plants. The carpospore on germination is diploid : it is inferred that it produces a tetrasporic plant (*sporophyte*), which after reduction bears tetraspores. The tetraspore on germination is haploid : it is inferred that it produces the haploid sexual plant (*gametophyte*). The haploid nuclei of spermatium and carpogonium on fusion lead to the formation of the diploid carpospores : and so on. There is thus a regular alternation of tetrasporic and sexual plants ; but in form these are closely alike. The case is comparable with that of *Dictyota*, and questions of the origin of alternation in the Red Algae are raised similar to those for the Brown. (See Chapter XXXII.)

CHAPTER XXV.

GREEN ALGAE (*CHLOROPHYCEAE*).

THE Brown and Red Algae form natural and coherent groups of plants, characterised by their colour, but more particularly by their propagative organs. Green Algae are a more heterogeneous assemblage of forms. Some are marine: others live in fresh water. Some are unicellular, some colonial (Protococcales, Volvocales): others, which are multicellular, consist of a simple filament, with various degrees of its branching (Ulothricales); or they may form widened flat expansions (Ulvaceae): others again are coenocytic, not being partitioned into cells (Siphonales), or only partially septate (Siphonocladiales). The variety of their form and structure is matched by the diversity of their propagation. Some multiply by simple fission (*Protococcus viridis*, Fig. 328): others undergo conjugation of equal, non-motile cells (Conjugatae); but most of them produce motile zoospores and gametes, the latter showing in more than one natural series evidence of a progressive sexual differentiation (Ulothricales, Siphonales, Fig. 335). The effect of a general study of them is to suggest that they may all represent steps in advance from the Flagellatae; and that they represent many distinct lines in which an increasing complexity of development of their encysted phase, and a differentiation of sex have been independently achieved.

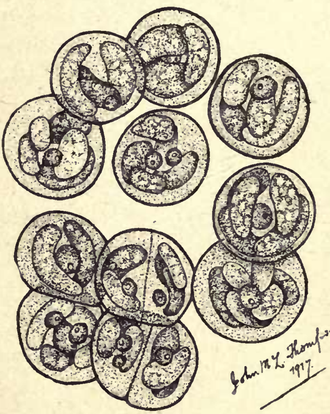


FIG. 328.
Cells of *Protococcus*, some isolated, others resulting from recent division, are still coherent. (× 730.)

A simple example of the Volvocales, a series of free-swimming organisms which retain their cilia in the vegetative stage, is seen in *Chlamydomonas* (Fig. 329). Each cell has a nucleus, a chromatophore with pyrenoid, an eye-spot, and two cilia by which it is actively motile. Externally is a swollen wall of cellulose. Multiplication is by zoospores formed by division of one cell into 2, 4, or 8 (Fig. 329, *b*). They are enclosed at first in the cell-wall, but finally escape as separate individuals. There is also sexual reproduction by pairing of similar biciliate gametes,—or in some species of dissimilar gametes,—to form a zygote. The sexual differentiation thus initiated in *Chlamydomonas* is carried to the point of distinct oogamy in *Volvox*, a larger spherical, free-swimming organism, in which, in addition to vegetative propagation of daughter-spheres within the parent, there are well-defined antheridia and oogonia. These organisms, which are sometimes described as animals, stand near to the Flagellatae, and illustrate progression both in vegetative structure and in sexual method.

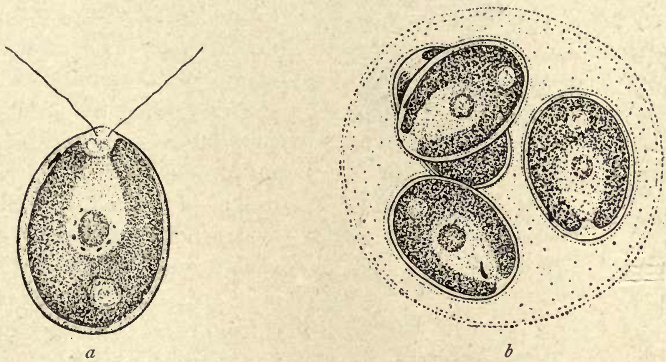


FIG. 329.
Chlamydomonas. *a*, unicellular plant motile by two cilia. *b*, result of division into four. (Dr. J. M. Thompson.)

In the *Protococcales* the vegetative cells are non-motile, though in some of them motile zoospores and gametes may be produced. A common and very simple example is seen in *Protococcus viridis*, Ag. (= *Pleurococcus vulgaris*), found as a green incrustation on the windward side of tree-trunks, etc. The plant retains its vitality after drying, as from its habitat it would need to do. Each cell is limited by a cell-wall, and contains a nucleus and a definite chloroplast, which being lobed gives the appearance of several, though it is stated that only one is really present (Fig. 328). Multiplication is by cell-division, the products of which remain loosely related to one another in groups; finally they separate by rounding off of the cells. No motile stage has been proved to occur. It is as though that plant represented an unlimited repetition of the encysted stage of a Flagellate, such as *Euglena*.

The *Ulothricales* are relatively advanced in development of their plant-body, owing to repeated cell-division, the products of which remain associated together to form filaments, as in *Ulothrix* or *Œdogonium*; or the filaments may be branched, as in *Bulbochaete*; or flattened expansions may be formed, as in *Ulva* or *Enteromorpha*.

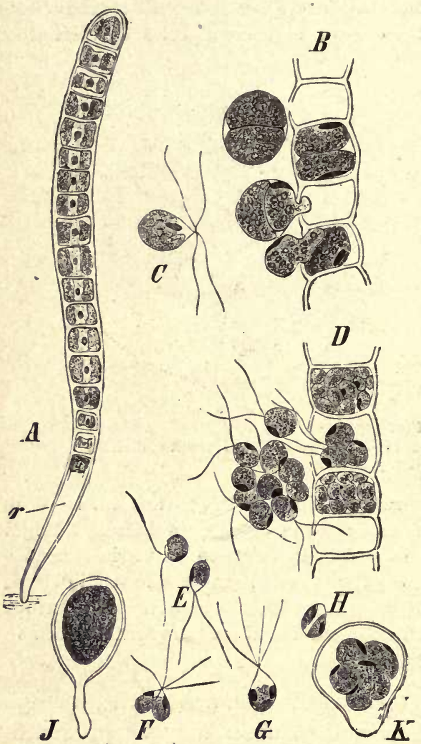


FIG. 330.
Ulothrix zonata. *A*, young filament with rhizoid *r* (× 300). *B*, portion of filament with escaping zoospores. *C*, single zoospore. *D*, formation and escape of gametes. *E* = gametes. *F* = conjugation. *G* = zygote. *H* = zygote. *J* = zygote after period of rest. *K* = zygote after division into zoospores. (After Dodel-Port.) (*B-K* × 482.) (From Strasburger.)

The plants inhabit salt or fresh water, or may even grow in moist air, as *Chroolepus* does. *Ulothrix* itself, which is commonly found attached to stones washed by a quickly running stream, serves as a simple example. Each unbranched filament consists of a series of discoid cells, each with a zonal chloroplast, and it is attached by a basal rhizoid (Fig. 330, *A*). Its propagation though varied is rudimentary like its vegetative structure. *Zoospores* may be produced either singly from a cell or by division of its contents, which escape through an opening of the cell-wall into the water (*B*). According to the number of the divisions the zoospores may differ in size. Each has *four cilia* attached to the narrower end of its pear-shaped body (*C*). After a period of movement they settle, form a cell-wall, and affix themselves to some solid substratum: growing out transversely to their former axis and dividing, each may form a new filament. The *gametes* are also produced in a similar way, but the divisions are more numerous, their size smaller, and they bear only *two cilia* (*E*). The gametes, which are all alike in size and form, escape from cells: if those from different filaments meet they coalesce in pairs, the result being a four-ciliate *zygote*, which soon loses its cilia, settles, and forms a cell-wall. After a period of rest it germinates, the contents dividing, and escaping as zoospores, which grow into new filaments.

Ulothrix takes a low place both as regards structure and propagative method. The differentiation of its sexual cells is imperfect. Not only is there no distinction of sex in the form of the gametes, but occasionally the gametes may themselves germinate without fusion. They are strikingly similar in form and origin to the zoospores. The facts are in accord with the theory that fusion of gametes (syngamy) is a means of strengthening otherwise weak cells, which were originally organs of vegetative propagation.

Oedogonium and Bulbochaete are also filamentous Algae, but with more elaborate structure of their cells. Various species are very

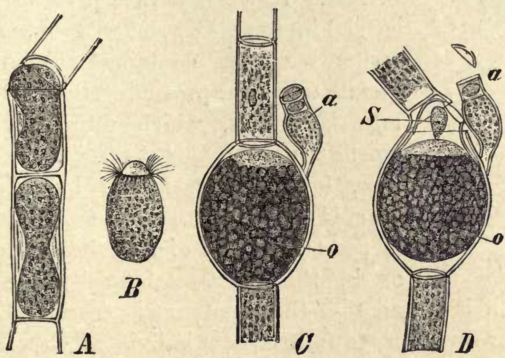


FIG. 331.
Oedogonium. *A*=escaping zoospores. *B*=free zoospores. *C*=sexual organs before fertilisation. *D*=in process of fertilisation. *O*=oogonia; *a*=dwarf-males. *S*=spermatozoid. (After Pringsheim, from Strasburger.) (×350.)

commonly found attached to stones or submerged parts of plants in quiet fresh water. Their cells are uninucleate, and contain a single reticulate chromatophore. They may be propagated by zoospores, which are formed from the whole content of a cell; it escapes through a transverse slit in the wall into water, having an oval form, with a fringe of cilia round the colourless anterior end (Fig. 331). After a period of movement the zoospore settles, forms a cell-wall, and grows directly into a new individual. The plants are readily distributed by this means. The sexual organs of *Oedogonium* are antheridia and oogonia, which differ in size. The *oogonium* is a large barrel-shaped cell, containing a single egg. It opens at maturity by a transverse slit, as in the liberation of the zoospores; but the *ovum* remains *in situ*, and is motionless (Fig. 331, *C*, *D*). At the same time cells, of the same or of a separate filament, undergo repeated divisions to form short discoid cells, which are the *antheridia*. Each, on opening in the same way, sets free two *spermatozoids*, the result of division of its protoplast. They resemble the zoospores in form, but are smaller. In some species special small plants (dwarf-males) are produced from small zoospores, which fix themselves in the neighbourhood of the oogonium, and dividing into a few cells, liberate their spermatozoids close to the opening (Fig. 331, *C*, *D*). Fertilisation follows by fusion of the spermatozoid at the receptive spot of the ovum, and the coalescence of the nuclei has been observed. The zygote forms a firm protective wall: it is stored with nutriment, takes a brown or red colour, and may enter a period of rest. Its germination presents a point of special interest. The outer wall bursts and the contents escape, contained within a delicate membrane. The protoplast then divides usually into four cells, which ultimately escape as motile zoospores (Fig. 332). This division into four, following on sexual fusion, suggests a process of reduction comparable to that seen in the tetraspores of *Polysiphonia* or *Dictyota*, or in the spore-mother-cells of Mosses and Ferns. But it is stated that the zygote may occasionally germinate without those divisions, to form a new individual directly, while an unfertilised oogonium may do the same. It would thus appear that the cycle of events is not so stereotyped here as it has become in more advanced plants.

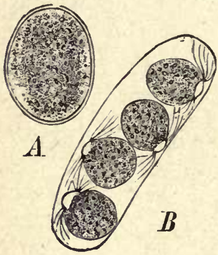


FIG. 332. *Bulbochaete intermedia*. *A* = oospore. *B* = formation of four zoospores in the germinating oospore. (After Pringsheim, from Strasburger.) (× 250.)

SIPHONALES.

The Siphonales have already been discussed in Chapter IX., in respect of their peculiar structure (p. 139, Fig. 98). They are *coenocytes*: that is, they are not partitioned into separate cells, but the plant-body consists of a large non-septate sac, limited by a cell-wall, and kept firm enough by internal turgor to preserve its form in the quiet water in which as a rule they live. This condition is shown in a less complete form in the Siphonocladiales, where septa occur at intervals, but the protoplasts lying between these are multi-nucleate, and hardly warrant their designation as cells. This is seen in *Cladophora*, a very common genus of fresh and salt-water Algae. Clearly the non-septate state is mechanically ineffective. It has been pointed out (p. 140) how, as a set off against it, the more complicated forms of the Siphoneae have acquired additional mechanical strength, either by internal cellulose ties, as in *Caulerpa* (Fig. 333), or by matting of their branches together, as in *Codium*, or by cementing those branches together, as in *Halimeda*. But these are concessions to an essentially weak construction. It is only possible to carry it to any considerable size when living in water, and all the larger forms are marine. *Vaucheria* is an exception: for though many of its species float in water, some live on moist soil, exposed to the air. But the members of the genus consist only of simple or branched filaments, and when living aerially they lie procumbent.

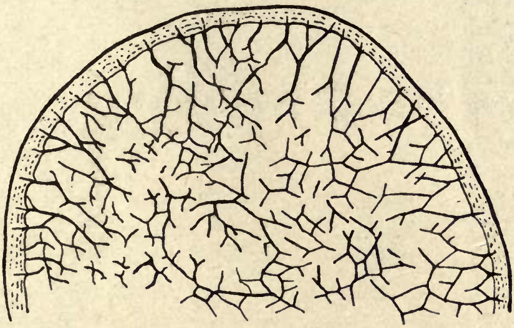


FIG. 333.
Part of a transverse section of *Caulerpa*, showing the thick outer wall, and the reticulate rods of cellulose, which act as ties, and give added rigidity. F.O.B. (×50.)

The cytoplasm of these plants contains many small chloroplasts, and numerous nuclei usually lying internally to them. Centrally is a large vacuole. In *Vaucheria* the product of photo-synthesis appears as oil, but others of the Siphoneae may contain starch, which is commonly present in Green Algae. The general physiology of a coenocytic, or as it has been called a non-cellular plant, is probably like that of any ordinary green plant. The difference lies in the mechanical construction.

Vegetative propagation is carried out in various Siphonaceous Algae by non-motile, or by motile cells, produced in large numbers in special branches, and liberated into the water. *Vaucheria* is an exception, in that the whole contents of such a branch-ending, which are previously shut off by a septum, are discharged as a single ciliated *zoospore*, large enough to be seen with the naked eye. The escape is effected in the early morning; after a period of movement the zoospore comes to rest, and germinates directly into a new plant

(Fig. 334). In structure the zoospore shows the cilia in pairs, each pair related to a nucleus which is superficial, while the chloroplasts lie within. The origin and structure of the zoospore suggests that

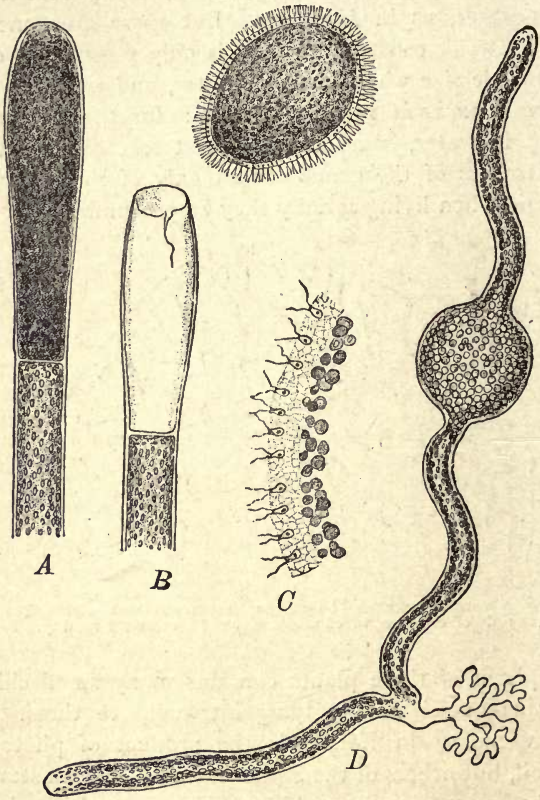


FIG. 334.
Vaucheria sessilis. *A*=young sporangium. *B*=zoospore, with the sporangium from which it has escaped. *C*=a portion of the peripheral zone of a zoospore. *D*=a young plant, with rhizoids, developed from a zoospore. (*A*, *B*, after Götz; *D* after Sachs; *C* after Strasburger.) (From Strasburger.)

it represents the undivided contents of a whole sporangium, such as may be seen in other Siphonales.

The Siphonales and Siphonocladiales reproduce sexually: but degrees of difference in size of the gametes are seen. The differentiation thus indicated must be held as distinct from, though parallel with that already described in the Brown Algae, and in the Ulothricales. In *Acetabularia* the gametes are of equal size, and those produced from different sporangia, or from different plants fuse in pairs (Fig. 335, i.). In *Bryopsis* the size is unequal (ii.); while *Codium* shows still greater inequality (iii.). This is again more marked in

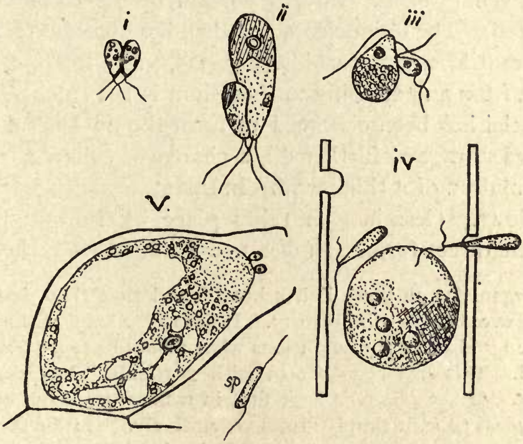


FIG. 335.
Gametes of various Siphonales, and Siphonocladiales, illustrating differentiation of male and female. i=*Acetabularia*, isogametes; ii=*Bryopsis*; iii=*Codium*; iv=*Sphaeroplea*; v=*Vaucheria*. In iv. and v. the large egg is stationary, while the smaller spermatozoid is motile. (Taken from Oltmanns' *Algae*.)

Sphaeroplea, where the large egg is non-motile (iv.), a condition still more accentuated in *Vaucheria* (v.), which is the most advanced of all in sexual differentiation.

The sex-organs of *Vaucheria* arise close together as short lateral branches (*V. sessilis*), or borne together on the same branch (*V. terrestris*, Fig. 336). The *antheridia* are horn-like, curved bodies, the *oogonia* are oval. In the antheridium a septum cuts off the multi-nucleate protoplast from the parent tube: each nucleus becomes the centre of a spindle-shaped spermatozoid; and these escape, with their paired cilia pointing fore and aft, through an opening at the distal end. The *oogonium* also at first contains numerous nuclei embedded in protoplasm stored with many globules of oil. But, as the ovum matures, all the nuclei but one wander back into the parent

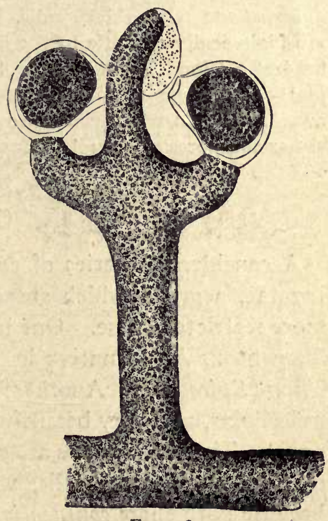


FIG. 336.
Sexual branch of *Vaucheria terrestris*, bearing distally a curved antheridium, and right and left oval oogonia.

filament, which is then shut off from the oogonium by a wall. Meanwhile a beak has formed at the distal end of the oogonium, which then opens by swelling of the wall, a portion of the colourless contents being emitted. The uninucleate egg then lies open for fertilisation by the small motile spermatozoids (Fig. 335, v.). It appears that self-fertilisation from an adjoining antheridium is the rule. The fusion of the two nuclei has been observed to form the nucleus of the zygote. Then follows storage of further oil, a change of colour of the contents, and the formation of a thick wall. In this state, as an *oospore*, a period of rest follows. Germination takes place by rupture of the thick wall, and the direct formation of a new filament from the contents.

In such organisms as these it has been found that there is no obligatory succession of events in the life-history. It lies in the hand of the experimenter to determine by altering the conditions what form of propagative organ shall be produced. This has been shown with particular clearness in the case of *Vaucheria.* If the plant be kept first in a flowing stream of water, as it may be in a glass tube, it simply grows vegetatively. If it be then transferred to still water, zoospores are produced. This also follows on flooding, in the case of terrestrial forms. If it be desired to produce sexual organs, the plant should be well nourished, for instance by exposure to good light, or cultivation in a weak sugar solution. A rise of temperature also encourages their production. Speaking generally, light produces sexual organs, shade zoospores. A third type of propagative organ is formed in some species (*V. geminata*). Under dry conditions the filament, dividing up into short lengths, forms *aplanospores* with thick walls. These can stand drying up. All of these are biologically suitable to the spread and survival of the plant in its native habitat. When flooded in cool weather it forms zoospores. When there is risk of drying up in summer after exposure to light and heat it forms zygotes or aplanospores, which can tide over the period of drought ; but on germination either zoospores or sexual organs may be formed according to the conditions.

CONJUGATAE.

A considerable series of common Green Algae belong to the Conjugatae, a group which stands aloof from the Chlorophyceae in the more restricted sense. One large family of these are the *Zygnemaceae*, filamentous Algae native in still water : the most familiar example being *Spirogyra.* Another family, the *Desmidiaceae*, are mostly unicellular, and very beautiful. They are found in quantities in peaty pools. The two families are grouped together because of the structure of their uninucleate cells, with complicated chromatophores ; and because both show *conjugation of non-motile gametes.*

The well-known genus *Spirogyra* includes numerous species, of which the filaments float commonly unattached in still fresh water, and with no distinction of apex and base. They are slimy to the touch, owing to their mucilaginous outer wall. Each filament is partitioned by transverse septa into cells, each of which may be detached from its neighbours by shock, when its convex ends demonstrate its internal turgor. Growing on and dividing, each may form

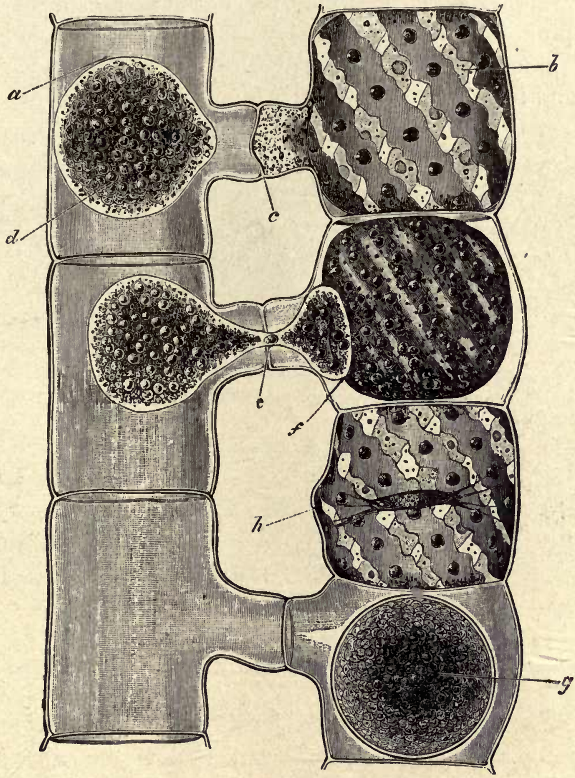


FIG. 337.

Two filaments of *Spirogyra*, which illustrate various stages of conjugation. *a*, *b*, have formed outgrowths which have met at *c*; the protoplast *d* is contracted to a dense sphere. The next lower pair of cells show conjugation, the protoplasts fusing at *f*. In *g*, conjugation is complete, a zygote having been formed by the fusion of two protoplasts. (After Kny.)

a new filament. Each cell is practically an individual (Fig. 337, cell *h*). It is cylindrical, the proportion of length to breadth varying in different species. Within the external wall is a layer of colourless cytoplasm surrounding a central vacuole, in the middle of which the single nucleus is suspended by colourless threads. The most marked feature is the green spiral chromatophore, which gives the genus its name. One or more of these, according to species, may lie embedded in the peripheral cytoplasm, coiled corkscrew-fashion. As in the Conjugatae generally, pyrenoids occur in the chromatophores: they are highly refractive, and form centres for the formation of starch, while the threads that suspend the nucleus usually run out to them.

Vegetative propagation is simply by division of the cells, which occurs during the night, and may be continued indefinitely. As the season progresses the filaments conjugate. Adjacent filaments put out processes from cells opposite one another, which meet, flatten, and fuse at their tips, the intervening wall being absorbed.

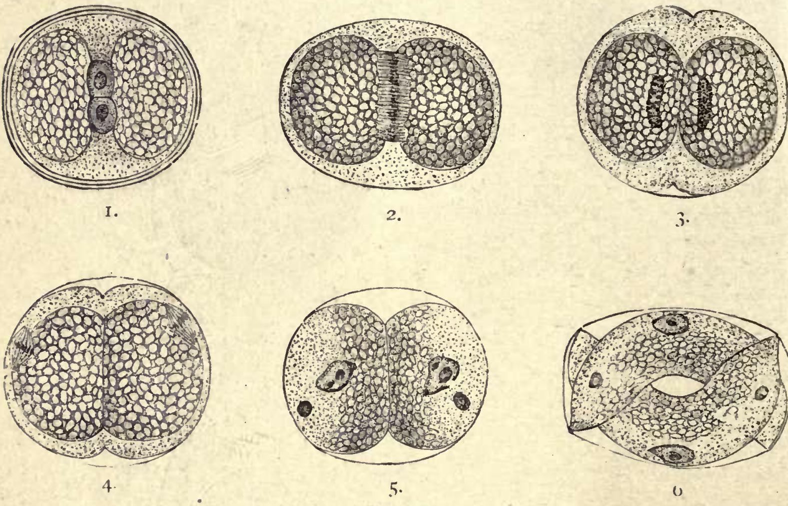


FIG. 338.

Germination of a Desmid, *Closterium*, after Klebahn. 1, zygote before nuclear fusion; 2, first nuclear division; 3, binuclear stage; 4, second nuclear division; 5, two cells, each with a small and a large nucleus. 6, formation of two new *Closterium* cells each with one large nucleus; the other is disorganised. (From Oltmanns.)

Their protoplasts contract, one earlier than the other; it then passes bodily through the now open tube, and its cytoplasm coalesces with that of the other cell, while its chloroplast disorganises (Fig. 337). The nuclei remain for a time distinct. The zygote changes to a reddish colour, fats are stored in it, and a thickened wall is formed. Freed from the parent filaments it remains dormant. On germinating the outer wall ruptures, while the inner covers the enlarging protoplast. The fused nuclei divide into four, but of these only one survives as the nucleus of the first cell, from which by division a new filament arises.

In *Mesocarpus* the conjugation is similar, except that the zygote is formed actually in the tube connecting the conjugating cells.

Conjugation in the *Desmids* is essentially similar. The behaviour of the zygote on germination has been followed (Fig. 338), and there also, after delayed fusion, the nucleus divides into two and then into four; but two are atrophied, while the others remain as the nuclei of the two new cells formed on germination. Thus in the Conjugatae there is a tetrad-division, and a presumable reduction which follows on conjugation, just as tetrad-division follows on sexual fusion elsewhere.

It is different in the *Diatoms*, a distinct family of unicellular Algae with very many forms, marine and fresh-water, great numbers of which are found in the floating "Plankton." Their chloroplasts are brown, and the uninucleate protoplast is enclosed between two silicified shells with delicate sculpturing, which fit over one another like the two parts of a pill-box. Vegetative division results in regular decrease in size of the cells, till a limit is reached, from which recovery is usually by conjugation, resulting in *Auxospores*. The nuclei of the conjugating cells of certain types, such as *Rhopalodia*, first divide into four: each cell then divides into two gametes with two nuclei in each of them, one large and one small: the gametes then fuse in pairs, the larger nuclei also fusing, while the smaller disintegrate. Here also there is a tetrad-division, but it *precedes* conjugation, while in the Conjugatae it *follows*. It may then be concluded that the vegetative period of the Conjugatae is haploid, while that of certain Diatoms is diploid; as it is also in *Fucus*. Such facts have their importance in questions to be discussed in Chapter XXXII.

Examples such as these from the Green Algae show how diverse those plants are in structure and in propagative method. It may be held that they sprang from some common source such as the Flagellates: and this would seem probable from their characters, both vegetative and propagative. But the differences which they show suggest a plurality of lines of parallel development. More especially does this emerge from their comparison in respect of sexual differentiation. The steps of distinction of male and female gametes correspond in the Volvocales, Ulothricales, and Siphonales, though these series are sharply distinct in vegetative structure. They also resemble the progression already traced in the still more distinct Brown Algae (p. 385). The only possible conclusion from such facts is that the distinction of the sexes has been achieved not only once, but in a number of distinct evolutionary series. There has in fact been *parallel development*, or as it is styled, *homoplasy*. The spermatozoids and ova of *Volvox*, *Œdogonium*, *Vaucheria*, and *Fucus* are not then to be held as *homogenous*, that is, produced from a common ancestry that bore spermatozoids and eggs; but *homoplastic*, that is, each has arrived as a result of independent sexual evolution from some ancestry, which had not male spermatozoids or female eggs but undifferentiated gametes as the propagative organs.

CHAPTER XXVI.

FUNGI. INTRODUCTORY.

The character which all Fungi have in common is a negative one: the *absence of chlorophyll*, or of any kindred colouring matter by means of which they can carry on photo-synthesis. They are therefore sometimes called colourless; but many of them, and especially the large Toadstools, are brightly coloured, though with pigments quite distinct from chlorophyll. The absence of chlorophyll is associated with the fact that they are able to acquire their supplies indirectly: that is, either by a *parasitic* or a *saprophytic habit*. These methods of nutrition have already been discussed in Chapter XI., as they are seen in Seed-bearing Plants. A mere negative character, such as the absence of chlorophyll, is not in itself a sound basis for classification. At once the doubt is aroused whether all the Fungi are really "blood-relations." Such Phanerogamic parasites and saprophytes as were described in Chapter XI. are without chlorophyll. But they are for the most part referable to well-known Natural Families, a fact which signifies that their ancestors were green, and that the parasitic or saprophytic habit was adopted relatively late in the Evolutionary History, after the seed-habit was already established. No one would suggest that these plants should be ranked as Fungi, nor assume that they are all "blood-relations."

It is probable a like story accounts for the origin of the Fungi, and that they also sprang from self-supporting ancestors. But there is reason to believe that at least the majority of them adopted irregular nutrition early. The opportunity for parasitism and saprophytism was open from the earliest times, wherever organisms grew closely crowded, or their decaying bodies were massed together. The study of fossil plants has shown that organisms characteristically fungal existed from the earliest geological horizons from which there is any reliable record. In the Lower Devonian, long before there were any Flowering Plants, there is abundant evidence of Fungal structure existing under conditions favourable to that habit. It does not, however, follow that all organisms which adopted a "fungal" habit early were allied to one another, nor that all Fungi originated at the same time. The existence of parasitic and saprophytic Seed-Plants is a warning against such an assumption. We should rather be prepared to recognise that "*Fungi*" *have originated along more than one line of Descent, and probably at different times, from very early periods onwards.* It is natural to seek for some Algal origin for them, for in many features they resemble Algae. At least two general sources can be suggested, though the actual points of connection by descent may have been numerous. One is *from non-septate Algae*, such as the Siphoneae. This has probably given rise to those *non-septate Fungi*, which are called *Phycomycetes*, from their Alga-like features. The other is *from septate Algae*; and there are various grounds for believing that the septate filamentous Red Algae gave rise to many at least of those *septate Fungi*, which are called the *Eumycetes.*

The lower organisms, and especially those of aquatic life, are habitually in close juxtaposition. As a rule any large Seaweed or submerged fresh-water plant bears innumerable smaller organisms attached to its surface. Sometimes they penetrate into its tissues. Some by preference frequent certain hosts. Thus *Polysiphonia fastigiata* is regularly borne on the Brown Tangle *Ascophyllum nodosum*, and its filaments extend deeply into its tissues. The proof of actual parasitism is here incomplete, though the regularity of occurrence arouses suspicion. But there can be no doubt of the physiological dependence in *Harveyella mirabilis*, which grows as a colourless parasite penetrating the tissue of *Rhodomela*, one of the Red Algae (Fig. 339). The parasite is by structure and propagative organs clearly another Red Alga, which acts like a true Fungus. Among the Green Algae, *Coleochaete*, one of the Ulothricales, grows habitually on the surface of submerged plants. The allied *Mycoidea parasitica*, though still green, penetrates the tissues of the leaves of *Camellia.* Other similar cases might be quoted from allied septate Algae. Again, the green Siphonaceous *Phyllosiphon* lives habitually in the intercellular spaces of the leaf of *Arisarum*, causing discoloured patches. Such examples, which might be greatly extended, show how juxtaposition may give opportunity for parasitic encroachment. They are seen in modern living forms referable to recognised groups of Algae. They suggest how in the past fungal parasitism may have arisen. They also prove that the "Fungal" condition may be arising now, as in the past, and along a plurality of evolutionary lines.

The Fungi are very various in habit, and in form. The most familiar types are the large Mushrooms and Toadstools,—or "seats of death," so called in allusion to their frequently poisonous character.

Many of these grow on decaying humus, and like the Common Mushroom are saprophytes. Others are parasites, like the large shelf-fungi (*Polyporus*), which grow out from the trunks of trees, and are the cause of the perishing of the heart-wood in hollow timber; or like the Honey-Agaric (*Armillaria mellea*), which kills forest trees by attacking their soft and nutritious cambium (Fig. 340). But

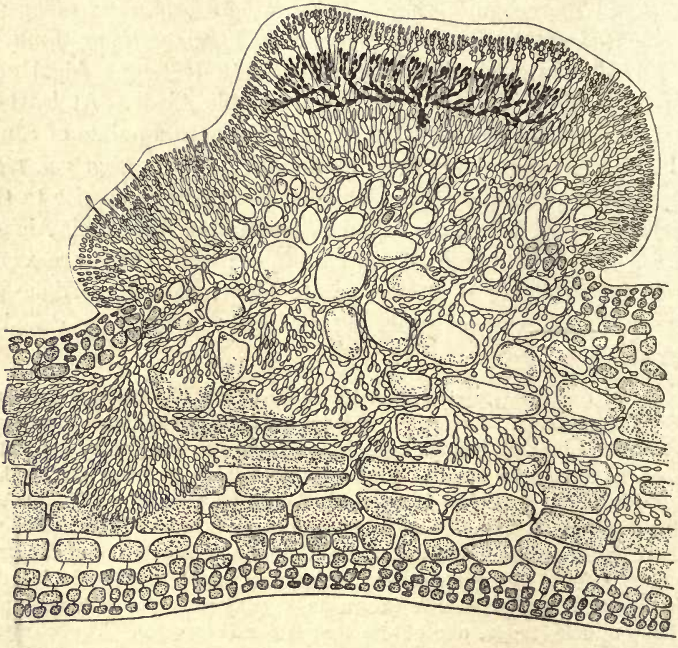


FIG. 339.

Harveyella mirabilis, growing as a colourless parasite on the thallus of *Rhodomela*, one of the Red Algae. Longitudinal section of *Rhodomela* bearing the parasite, with a mature cystocarp, the fertile filaments of which are black. The cells of the host with food-material are dotted; those which are exhausted are left blank. (After Sturch.)

apart from these there are multitudinous smaller Fungi, such as the parasitic Mildews and saprophytic Moulds, while the unicellular Yeasts show the simplest structure of them all. However complicated and various their structure may be, it is based upon the *simple or branched filament*, *or hypha*. The whole system of such hyphae is called a *mycelium*. Such filaments may grow singly, as in the Moulds and Mildews, or they may be massed together so as to form the complex bodies of the larger Fungi. When closely appressed the septate filaments may seem to form a definite tissue; but it is in origin always a *false tissue*, or *pseudo-parenchyma*, made up from independent filaments, not a true parenchyma produced by segmentation of cells with a common origin. Many Fungi form large solid masses of such pseudo-parenchyma, which are called *sclerotia*, and serve for storage during a resting period (Fig. 341). The hyphae are limited by a cell-wall, composed of substance differing in its reactions from ordinary cellulose: they may be septate or non-septate, and in

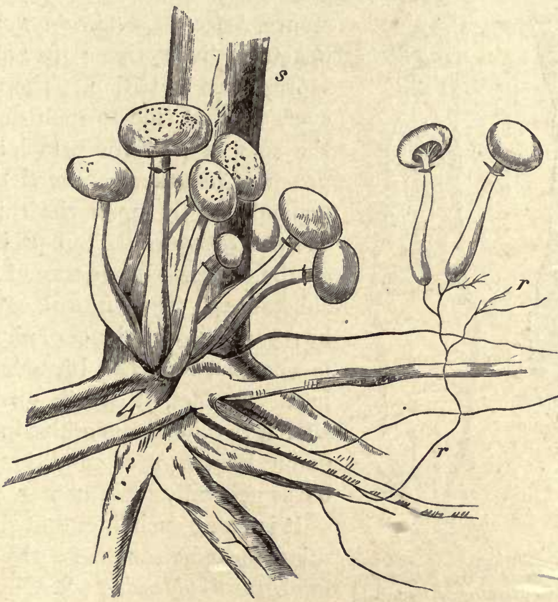


FIG. 340.
Base of a young tree (*s*) killed by *Armillaria mellea*, which has attacked the roots, and developed rhizomorphs (*r*) and fructifications. To the right the fructifications have been traced by dissection to the rhizomorphs that produced them. (After Marshall Ward.)

the former case there may be considerable variety in the number of the minute nuclei in their colourless protoplasts. Chromatophores are absent, and there is no starch, its place being taken by *glycogen*, or by globules of oil. Thus structurally the cells of Fungi resemble those of Algae, but without the chloroplasts or chlorophyll.

The success of the Fungal nutrition, whether parasitic or saprophytic, depends greatly upon their *power of penetration* of the nutritive medium. It has been shown in various cases that this is due to a digestive secretion, and the same probably applies generally. A highly refractive drop may sometimes be seen on the end of the hypha, which is believed to contain a *digestive ferment* (Fig. 342, i. ii.). A ferment has been extracted from large cultures of a certain *Botrytis*, and found to act upon cell-walls, causing them to swell. Such swelling is a feature of the perforation by the invading hypha, which first softens the cell-wall, and then seems to sink into the softened mass, finally emerging on the other side (Fig. 342, iii.-viii.). This power of perforation has been found in certain cases to depend upon the nutrition of the Fungus: for instance, *Sclerotinia sclerotiorum* can only penetrate living tissue after a period of saprophytic nutrition. There is, however, another side to such questions in the case of parasitic attack: viz. the power of resistance of the victim, which depends partly upon the thickness of the protective walls, but probably also on the presence or absence of inhibiting substances. Thus fungal attack may be regarded as a balance of physiological powers between the invader and the host. In fact, it stands on a footing similar to that of mycorhiza in Phanerogamic Plants, or of conditions of symbiosis generally (see Chapter XI.).

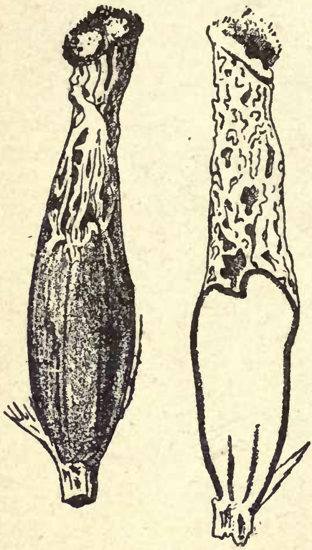


FIG. 341.
Sclerotium of Ergot of Rye (*Claviceps*), a mass of pseudo-parenchyma formed in the ovary of Rye: above is the style still covered by remains of "Honey-Dew" (see p. 437).

It is along such lines that the explanation must be sought for the condition known as "*epidemic*," where by a sudden outburst a disease becomes prevalent. Examples have been seen in the Irish Potato Famine, the Coffee-Disease of Ceylon, or the Lily-Disease which in 1888 made the cultivation of Lilies in the Thames Valley a failure. In such cases the disease is not necessarily a new one. The novelty lies in the success of the invader. It appears to be due to a change of balance between attack and resistance. That balance may be affected either by physiological strengthening of the parasite, or by weakening of the host. Sometimes the same circumstances may affect both. In the Lily Disease and the Potato Disease a cold wet season, while it favours the fungus, produces a thin-walled, watery host, readily susceptible to attack. A similar epidemic of "damping off" by *Pythium* may at any time be induced by cultivation of Cress overcrowded, in moisture and heat (see p. 413).

The effect of the parasitic invasion may be the death of the host, where vital parts are destroyed, as in attacks by *Pythium*, or *Armillaria mellea* (Fig. 340). But in many cases the attack is tolerated by the host, with only partial injury. It is often the leaf, or only certain tissues of the leaf, which are attacked, the result being a loss of efficiency by the host, while the parasite gains access to the sources of supply. These may indeed be stimulated to greater action, with the effect of swelling, and extra divisions of their cells. The result may be various *malformations*, such as are seen in the familiar leaf-curl of Peaches, or the swollen patches of Cluster-Cups (Fig. 383, p. 447).

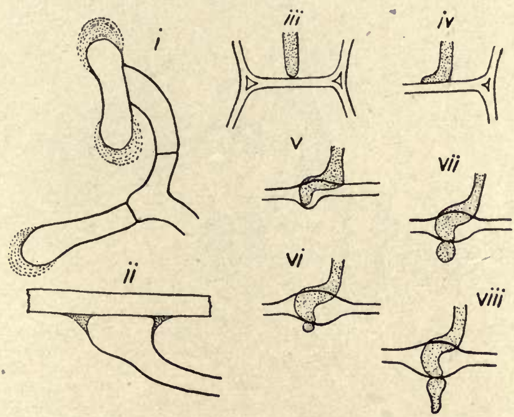


FIG. 342.

Successive stages of the penetration of cell-wall of Lily by the hypha of the Fungus causing the Lily disease. (After Marshall Ward.) See Text, p. 406.

The attack may, however, be upon the stem or root, or even the ovary. The effect is to produce swellings and malformations such as those of the roots of Crucifers, called "Club-root" (Fig. 343), or of the grain of "Ergot of Rye" (Fig. 341).

Some Fungi lead a constantly parasitic life, as the Rusts (Uredineae) do. Others are as constantly saprophytic, like the Saprolegniae. Others again may be sometimes the one, sometimes the other: and this may be so in the individual life. Thus *Pythium*,—the "Damping-off Fungus," attacks the seedling-host, and kills it, but continues to live on the corpse (p. 413). It is first parasitic, then saprophytic. But the converse has been shown in *Sclerotinia sclerotiorum*, where a period of saprophytic nourishment is a necessary condition for its success in perforating the living host. It has been regarded as a Fungus which is in course of "education" for passage from the saprophytic to the parasitic life. It is thus impossible to lay down any general rule of priority for parasitism or saprophytism: and it is only in certain cases that the one habit or the other can be assigned to any definite systematic group.

The life of Fungi is very varied. No organisms show greater resource in the acquisition of food. But their propagative methods are no less effective. Originally sprung from aquatic organisms, some show this clearly in their reproductive organs, which often involve motility in external *water*, as in many Phycomycetes. But the more advanced types are commonly propagated by means which are clearly

FIG. 343.
Portion of the root of a Crucifer malformed owing to the presence of *Plasmodiophora*. (After Woronin; from Marshall Ward.)

related to life in the *air*. In most Eumycetes minute bodies called *conidia* are borne in prodigious numbers, and they are small enough to be carried as dry dusty bodies through the air. The conidia of common Moulds are present everywhere about the dwellings of man: so that any suitable medium is apt to be invaded by them, provided the conditions of temperature and moisture are favourable. This explains the apparently spontaneous appearance of moulds on bread, leather, jam, etc., when kept in a confined space. The spread of fungal diseases is usually by similar means. One of the most surprising facts in this relation is the very constant recurrence of certain Fungi on isolated and restricted media. The horns of sheep cast away on a Scottish hill-side are commonly invaded by a horn-destroying Fungus, *Onygena*. But any one such horn may be isolated far from any visible source of infection. This shows the ubiquity of fungal spores. It suggests also the other side of the question, the vast number of germs that never find the suitable *nidus*.

Like other Thallophyta, Fungi may bear *organs of sex*, which lead up to the production of certain types of spore (*carpospores*). They thus show a life-cycle with successive stages comparable with that of autophytic plants. But in many of those which are regarded as the most advanced, and especially in the larger Agarics, sexual propagation is not normally carried out, and the organs of sex may be actually absent. Various stages of functional perversion, and of atrophy of the sexual organs, are illustrated by less advanced Fungi. Most Fungi have thus two forms of spores in their life-history, *conidia*

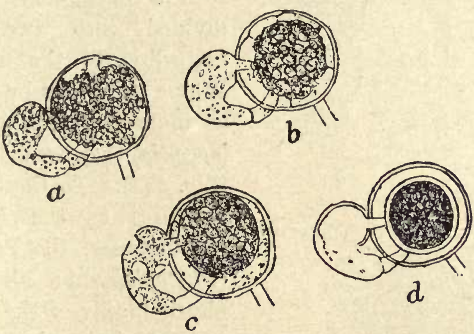


FIG. 344.

Development and fertilization of the ovum of *Pythium*. The granular protoplasm of the oogonium (*c*) collects into a ball, and the antheridium sends in a fertilising tube. In (*b*) and (*c*) transmission of contents into the ovum is shown. (*d*) The ovum has formed a cell-wall, and lies loosely in the oogonium. Highly magnified. (After Marshall Ward.)

and *carpospores*: some of them have more than two. These being borne on distinctive bodies, such as conidiophores or spore-fruits, differ in appearance, though they are really stages in one life-story. Sometimes in parasitic Fungi these stages may appear on different hosts, as in the Rust of Wheat, where the one stage is on the Wheat another on the Barberry (p. 442). Naturally, before the facts were fully known, such stages were liable to be regarded as different Fungi, and described by distinct names. For instance, the Rust on Wheat was called *Puccinia*, while the stage on the Barberry was described as *Aecidium*. Later these were proved to be merely parts of the same life-history, and they were given a single designation. But in many Fungi the life-history is not yet fully known, often because one stage is commoner, or more obvious than another. Those Fungi in which the knowledge of the life-cycle is incomplete are called

"*Fungi Imperfecti*," and they constitute a large proportion of the described species.

It will be gathered from the preceding pages that the Fungi provide characters, vegetative, propagative, and also functional, which will serve for their classification, though the data may often be insufficient for a final decision. Those Fungi which have *non-septate hyphae* are called PHYCOMYCETES. Their structure is relatively coarse, and corresponds in this, as well as in the absence of septa, to what is seen in the Siphoneae. They are divided into two sub-classes, according to the sexual organs. Where these can be distinguished as male (*antheridia*) and female (*oogonia*) they are called *Oomycetes* (Fig. 344). To these belong such parasites as the *Peronosporeae*, for instance, the Potato Fungus (*Phytophthora*); also the saprophytic family of the *Saprolegniae*, which includes the "Damping-off Fungus" of seedlings (*Pythium*). The latter live on vegetable or animal matter decaying in water. In the second sub-class there is *conjugation* of similar bodies to form a *zygospore*, as in the common Mould, *Mucor* (Fig. 345). These are designated the Zygomycetes, and they are also referable in origin probably to Algae of the type of the living Siphoneae. The Phycomycetes are dealt with in Chapter XXVII.

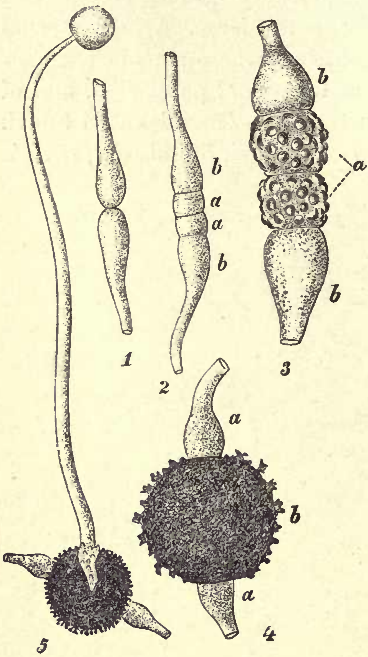


FIG. 345.

Mucor mucedo. Different stages in the formation and germination of the zygospore. 1=two conjugating branches in contact. 2=septation of the two conjugating cells. 3=more advanced stage; the conjugating cells are still distinct from one another. 4=ripe zygospore (*b*) between the suspensors (*a*). 5=germinating zygospore with germ-tube bearing a sporangium. (After Brefeld.) (1-4 × 225; 5 × *circa* 60.) (From v. Tavel.) (From Strasburger.)

The great bulk of the Fungi are probably distinct in Descent from these. The structural distinction lies in their *septate hyphae*. The constituent "cells" between the septa vary in length and in nuclear condition. In some cases the nuclei are small and numerous: in others there are a pair of nuclei, or only one. These septate Fungi are called the EU-MYCETES. The sexual organs of some of them indicate a probable origin from organisms like the Red Algae: for they have a *female carpogonium* with *trichogyne.* But in many of them such organs of sex have not been found, and there is reason to believe that they are no longer sexually produced. They are divided into two sub-classes, according to the method of production of their spores. In the first the spores, commonly eight in number, are produced internally within a closed body, the *ascus.* These are called

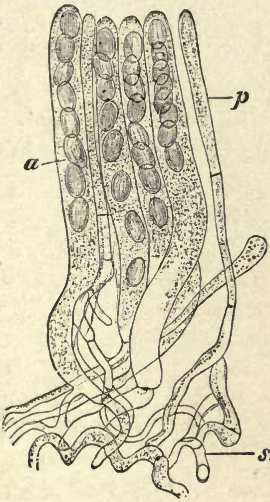


FIG. 346.

Portion of the hymenium of the Morel (*Morchella esculenta*). *a*=asci, each containing eight ascospores. *p*=paraphyses. *sh*=subhymenial tissue. (× 240.) (After Strasburger.)

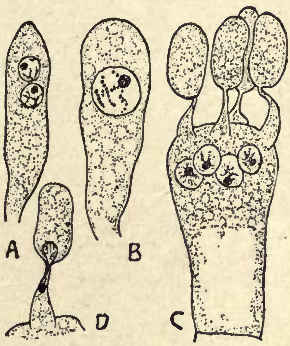


FIG. 347.

Honey Agaric (*Armillaria mellea*). *A*, young basidium with two primary nuclei. *B*, after fusion of the two nuclei. *C*=a basidium of *Hypholoma appendiculatum* before the four nuclei derived from the secondary nucleus of the basidium have passed into the four basidiospores. *D*=passage of a nucleus into the basidiospore. (After Ruhland.) (From Strasburger.)

asco-spores, and the sub-class the *Ascomycetes* (Fig. 346). To them belong many Moulds, Ergot of Rye, the edible Truffle, etc. Examples will be described in Chapter XXVIII.

In the second sub-class the spores are produced externally, commonly to the number of four, upon a body called a *basidium.* They are called *basidiospores*, and the sub-class the *Basidio-mycetes* (Fig. 347). To them belong the Mushrooms and Puff-balls; also the large series of parasitic Rusts, which being more primitive in their characters than the rest, give probable clues to the origin of the Basidiomycetes. They will be described in Chapter XXIX.

The Fungi may then be grouped thus:

Class.	Sub-Class.	Examples.
Phycomycetes (non-septate)	*Oomycetes*	*Pythium*, *Phytophthora*.
	Zygomycetes	*Mucor*, *Empusa*.
Eu-mycetes (septate)	*Ascomycetes*	*Sphaerotheca*, *Eurotium*, *Peziza*.
	Basidiomycetes	*Puccinia*, *Ustilago*, *Agaricus*, *Boletus*, *Scleroderma*.

CHAPTER XXVII.

PHYCOMYCETES.—(*a*) OOMYCETES.

Two of the commonest and most destructive of fungal parasites will serve to illustrate the Oo-mycetes. They both belong to those non-septate Fungi which habitually produce distinct male and female organs, comparable to those seen in the higher Siphonaceous Algae, such as *Vaucheria*. Like them also they include in their life-history a stage where zoospores are motile in water. This, together with their close dependence upon moisture during vegetation, justifies for them the name *Phycomycetes*, or Alga-like Fungi.

THE "DAMPING-OFF FUNGUS" (*Pythium debaryanum*).

When Mustard and Cress are sown thickly, and kept too warm and damp, the seedlings are liable to the disease of "damping-off," the plants quickly rotting with an unpleasant smell. Many other seedlings, and especially Cucumbers and Melons, are subject to it; in fact, the disease is one of the commonest difficulties of the gardener, and ruins the efforts of many amateurs. It makes its appearance at definite spots in the seed-beds, and if not checked it spreads thence in ever-increasing circles. The first sign is the collapse of a seedling, owing to the shrinking of its cortex, usually at some point above the soil-level, the stem being no longer able to support the weight above (Fig. 348). If the diseased plant be examined microscopically its tissues will be found to be riddled through and through by rather coarse colourless threads, enclosed by a cell-wall and filled with

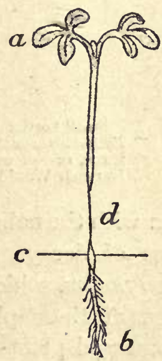


FIG. 348.
A young Cress-seedling attacked by *Pythium* at *d*, just above the ground-line *c*. *b*=root. *a*=cotyledons and plumule. (Nat. size.) (After Marshall Ward.)

granular protoplasm. The threads traverse the cell-walls of the host with the greatest ease, while collapse of the cells and loss of mechanical firmness lead to the falling over of the diseased plant (Fig. 349). Left to itself in moist air the disease may spread from plant to plant, the hyphae passing out from the tissues and forming cottony growths through the damp air: they are coarse enough to be

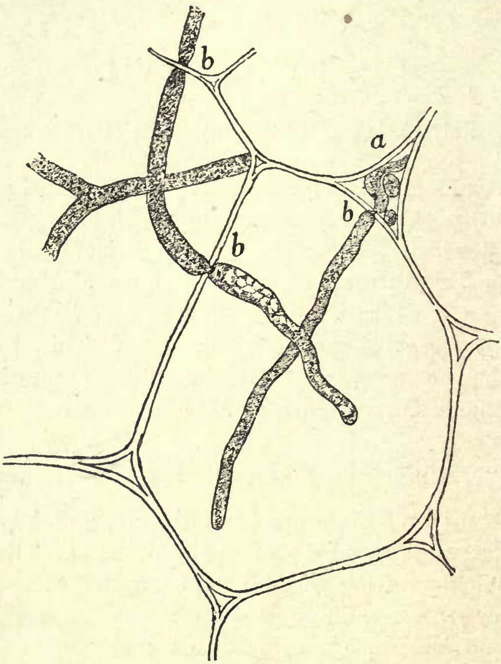


FIG. 349.

Small portion of cellular tissue of a *Potato*, showing the passage of the hyphae of *Pythium* through the cell-walls at *b*. At *a*, hyphae are seen in an inter-cellular space, one of which has then entered the large cell. Highly magnified. (After Marshall Ward.)

seen with the naked eye. The affected seedlings soon become a putrid mass of decay. The fungus that causes the trouble is *Pythium debaryanum*, which belongs to the large family of the Saprolegnieae. Most of these plants live actually in water, and cause decay in submerged plant- and animal-matter. One of them, *Achlya*, appears with a high degree of certainty on dead flies, if left floating in foul water.

Pythium propagates both vegetatively and sexually. The vegetative propagation is by sporangia (Fig. 350, *c*) formed usually from the ends of the hyphae, by their swelling to an oval form, their storage with fine-grained protoplasm, and being shut off by a septum. The

FIG. 350.
Portion of tissue near *d* in Fig. 348, highly magnified. The hyphae are seen running in all directions; at *a*, one passes through a stoma; at *c*, a sporangium is about to form. (After Marshall Ward.)

sporangium is readily detached, and germinates directly if the circumstances are favourable. It then grows out into a fresh hypha, which may directly infect a new victim. If one is not within reach, the germinating filament may expand into a spherical *zoo-sporangium*,

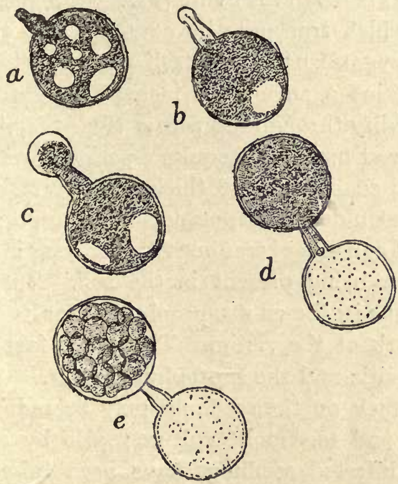


FIG. 351.
Germination of a sporangium of *Pythium debaryanum* in water. The tube put forth at *a* begins to swell at the end (*b*, *c*), and dilates (*d*), receiving all the protoplasm, which rapidly breaks up into zoospores (*e*). The whole process occupies about a quarter of an hour. Highly magnified. (After Marshall Ward.)

and the contents passing into it undergo division into a number of *zoo-spores* capable of movement (Fig. 351). These escape by rupture of the wall as minute colourless, kidney-shaped bodies with two active cilia. Provided there is water as the medium, they can seek out and even climb up the stem of other seedlings, and, coming to rest, perforate the superficial cell-walls, causing a new infection. It is in this way that the attack commonly appears some way up the stem. This method of propagation may be continued throughout the season.

But it is found that the disease is liable to reappear in a following year in seedlings grown on soil that has been badly affected before. This has been explained by the discovery of an alternate mode of *sexual propagation*, which produces *oospores*: these retain their vitality through the winter. If an infected plant be kept moist, or even immersed in water for a few days, the hyphae begin to form swellings at their ends, like the sporangia but larger (*oogonia*). Presently in these the protoplasm begins to draw away from the wall, and rounds off as a central sphere (the *ovum*). Meanwhile another branch, or the end of another hypha, grows up with a smaller swelling, which is also cut off by a septum (the *antheridium*). It comes into contact with the first, and puts out a slender tube which penetrates the cell-wall and extends to the ovum (Fig. 344, *b*, p. 409). This is the *fertilising tube*, which transmits its contents into the ovum. After fertilisation the zygote surrounds itself with a cell-wall, which soon thickens, but retains a smooth surface. This is the *oospore*, which can retain its vitality through the winter (Fig. 344, *d*). The oospores will not germinate at once, but require a period of rest. In the spring under favourable conditions the thick wall bursts and a hypha is produced, which soon develops sporangia and zoospores as usual. The initial infection of cultures of seedlings in each year is from this source, the resting spores being present in the soil. But besides this the fungus can continue its life as a saprophyte: for its activity does not end with the death of the victim. There is in fact no absolute line between the parasitic and the saprophytic habit.

The risk of attack on the seedlings may be reduced by avoiding too close sowing and too moist culture; also by avoiding the use of soil in which infected seedlings have been raised. Or the risk may be further reduced by raising the soil before sowing to a temperature that will kill all the spores that it contains.

The Potato Fungus (*Phytophthora infestans*)

The Potato Fungus is the cause of what is commonly known as the "Potato Disease," which is always a risk to the crop in damp, warm seasons. In the years 1845-1850 the disease already known in America assumed epidemic virulence in Ireland, causing the great famine. Since that time the Potato crop has never been entirely free from it. The disease makes its appearance upon the leaves and stems as spots at first small and pale-coloured, but as they enlarge the centre of each becomes brown, and extends, though still with a pale margin, till the spots run together, and the whole leaf or even the whole shoot may be affected (Fig. 352). If leaves with young infected patches be examined on a damp still day, or better, if they be kept in moist still air under a bell-glass, white glistening

FIG. 352.

A Potato-leaf, showing the spots and patches of "Potato-disease," due to *Phytophthora infestans*. In the darker patches the tissues are quite dead. The margins of the spots would show the hyphae of the fungus projecting from the surface. (After Sorauer; from Marshall Ward.)

filaments bearing white powdery *conidia* will be found on the lower surface. They are large enough to be seen with the naked eye, and are the *conidiophores* of the fungus. They spring from the mycelium, which permeates the mesophyll of the leaf in the diseased patch (Fig. 353). The mycelium consists of coarse non-septate, branched hyphae, which traverse the intercellular spaces, coming into close contact with the moist walls of the cells. They are also able to penetrate the softer middle-lamella of the cell-walls, where two cells adjoin, and this brings them into still closer relation to the cells, and the nourishment which these can supply (Fig. 354). Though the cells are not as a rule perforated, they lose their vitality and collapse, probably owing to a toxic influence. The brown discolouration at the centre of the infected spots is due to their decay.

The rapidity of the spread of the disease is one of its most surprising features. The fact that it habitually spreads down the prevailing wind indicates that it is due to wind-borne conidia. The *conidiophores* project through the stomata on the lower surface of the leaf and branch repeatedly (Fig. 353). The end of each branch may swell into an inverted pear-shaped *conidium*, which is constricted off from

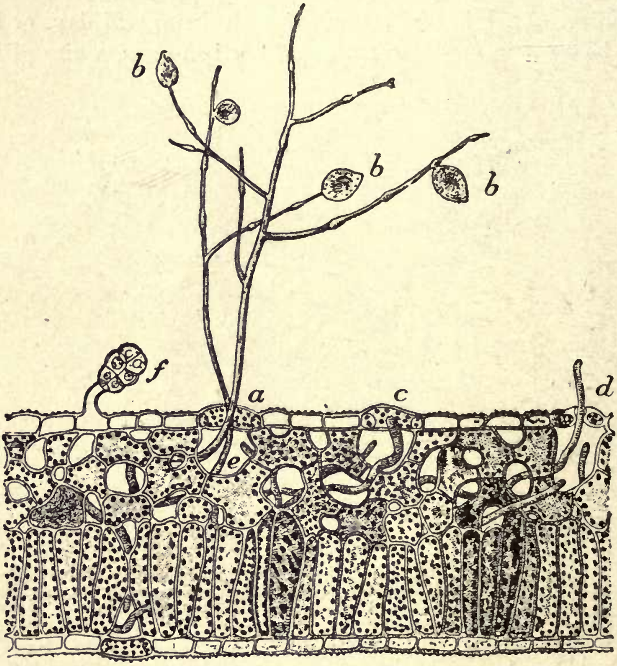


FIG. 353.

Section of Potato-leaf, in the tissues of which is the mycelum of *Phytophthora*. The hyphae run between the cells and send out through the stomata, *a*, *c*, *d*, the aerial branches which bear the conidia, *b*. The dark parts of the tissue of the leaf show where the cells are dying from the effects of the parasite. Highly magnified. The normally upper surface of the leaf is here turned downwards. (After Marshall Ward.)

its very thin stalk. If growing in still air the first conidium may be turned aside, the stalk growing on sympodially, and proceeding to form a second conidium, and so on. Thus a succession of conidia may be produced for a considerable time, each readily detachable, and easily borne by the wind.

Germination takes place only in presence of moisture. The protoplasm of the conidium divides into about ten parts, which escape by rupture of its apex into the water in the form of *zoospores*, very like those of *Pythium*, they are motile for a time by means of two cilia (Fig. 355). Coming then to rest, the cilia are dropped: each zoospore rounds itself off, and, investing itself with a wall, puts out a hyphal tube. If this takes place on the surface of a potato leaf, as it well might do under conditions of rain or heavy dew, all is ready for the infection. This may either be by entry through the pore of a stoma or by direct perforation through the epidermal wall (Fig. 356). By either route the parasite may reach the intercellular spaces and establish a new infection.

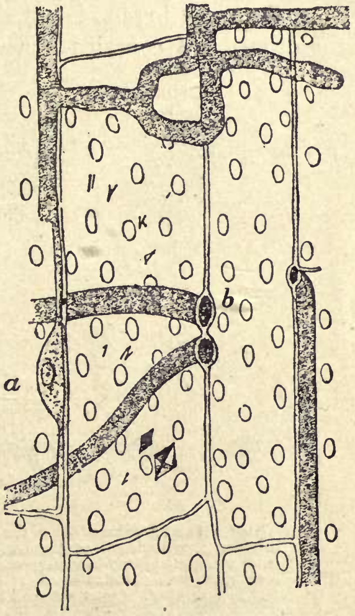


FIG. 354.
Piece of the tissue of the stem of a Potato-plant, showing the hyphae of *Phytaphthora* penetrating the middle lamella of the cell-walls. *a*=nucleus of a cell. Highly magnified. (After Marshall Ward.)

It is not only the leaves but also the stems and tubers of the Potato-plant that may be traversed. The mycelium spreads through the tissues down the haulms to the tubers. A perforation of the young tubers by a new infection from conidia is even possible, so long as their skin is thin. In bad cases tubers thus infected may decay at once. More commonly the hyphae enter a dormant state, and in this condition the tubers are harvested. But such tubers often decay during the winter. If, however, they are not heavily infected, and thus escape decay, and they are used as "seed" potatoes for a new crop, the young plants start infected from the first, and a recurrence of the disease is inevitable. The measures to be taken are to destroy by fire all infected haulms and leaves, to avoid carefully the use of tainted "seed" tubers; and, as a preventive, to spray the young growing crop with suitable disinfectants, especially if the season is wet in the middle summer. But a more hopeful line of prevention is by the use of "immune varieties," which are able to resist the attack of the parasite.

No mention has been made of sexual reproduction in the Potato Fungus. As a matter of fact sexual organs have not been proved to exist in *Phytophthora infestans* under normal conditions of life. Like some other plants it seems to be able to propagate itself indefinitely without the recurrence of sexual reproduction. But in other members of the Peronosporeae the details which have been observed show a striking parallelism with those of *Vaucheria*. The sexual organs have been found in *Peronospora* and *Albugo* to be formed within the host-plant (Fig. 357). The *oogonium* appears as a spherical swelling on the end of a hypha, while a thinner branch, arising as a rule below it on the same hypha, forms the *antheridium*. Each is shut off by a septum, and contains dense protoplasm with numerous nuclei.

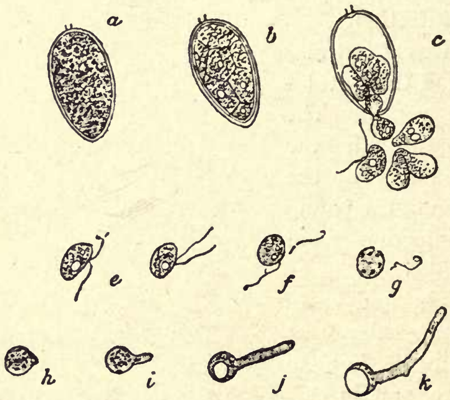


FIG. 355.
Stages of germination of one of the conidia of *Phytophthora*. *a*, the ripe conidium in water. *b*, protoplasmic contents breaking up into blocks, which separate and escape (*c*, *d*) as minute kidney-shaped zoospores (*e*), each with two cilia. *f*, *g*, the zoospore coming to rest, and losing its cilia. *h*, *i*, *j*, *k*, stages of germination of the zoospore. Highly magnified. (After Marshall Ward.)

A single egg, or ovum, is differentiated in the middle of the oogonium, by passage of all the nuclei but one to a peripheral position. The *uninucleate ovum* is then delimited from the *multinucleate periplasm*. The antheridium then penetrates the oogonium by means of a *fertilising tube*, the apex of which opens into the ovum, and transmits a single male nucleus (Fig. 357, *a*). The resulting zygote soon surrounds itself with a membrane, while the periplasm contributes to the thickening of its wall. A period of rest may ensue. On germination the contents of the zygote divide, giving rise to a number of zoospores, which may cause a fresh infection in the same way as those produced from the conidia.

The parallel between this structure and that of *Vaucheria* is close as regards the origin of the uninucleate ovum. The method of fertilisation by a fertilising tube in place of the liberated spermatozoids moving freely in water, offers an interesting parallel with the pollen-tube in Seed-Plants. In both cases the male gamete is conveyed to the female by a method suitable for land-living plants. Comparison shows that both are modifications of organs originally developed to secure fertilisation through the medium of external water. The question will naturally arise whether any fungal type still shows a motile male gamete. This is found in *Monoblepharis*, a fungus that lives saprophytically in water (Fig. 358). Here a terminal oogonium

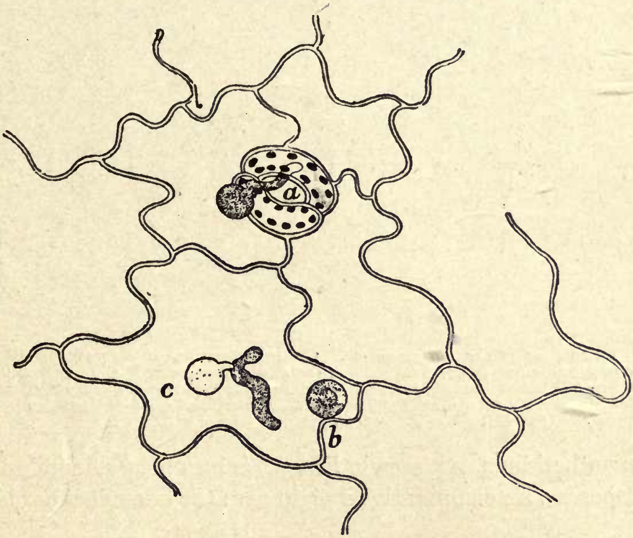


FIG. 356.
Germination of zoospores of *Phytophthora* on the epidermis of Potato. At (*a*) the germ-tube is entering a stoma. At (*c*) it bores directly through the cell-wall. Highly magnified. (After Marshall Ward.)

contains a single ovum, which is fertilised by spermatozoids, each motile by a single cilium. This case is unique among Fungi. It holds a place comparable with the motile spermatozoids of the Cycads and Ginkgo, as evidence of the transition from an aquatic to a terrestrial type of fertilisation. (Compare Chapter XXXII.)

The origin of such Phycomycetous Fungi as those described was probably from some Siphonaceous source. In the case of parasites the first step would be the adoption of an endophytic life, as in *Phyllosiphon*. This would be naturally followed by parasitic nutrition and loss of chlorophyll and chloroplasts. As regards the propagative organs, the conidium of *Pythium* or of *Phytophthora* represents a zoo-sporangium modified for separation and transport through the air. But it shows its real nature on germination by producing zoospores which are liberated in water. The modification of

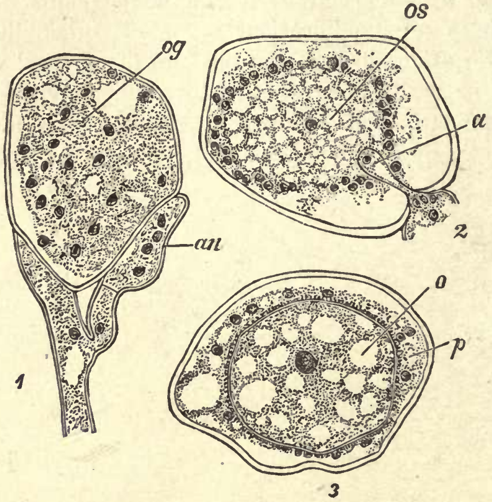


FIG. 357.

Fertilisation of the Peronosporeae. 1. *Peronospora parasitica*, young multinucleate oogonium (*og*), and antheridium (*an*). 2. *Albugo candida*. Oogonium with the central, uni-nucleate egg (*os*), and the fertilising tube (*a*) of the antheridium which introduces the male nucleus. 3. The same. The fertilised egg (*o*) surrounded by periplasm (*p*). (After Wager. ×666.) (From Strasburger.)

such an antheridium as is seen in *Vaucheria* into the pollinodium of the Peronosporeae, is a comparatively slight one: the latter does not liberate

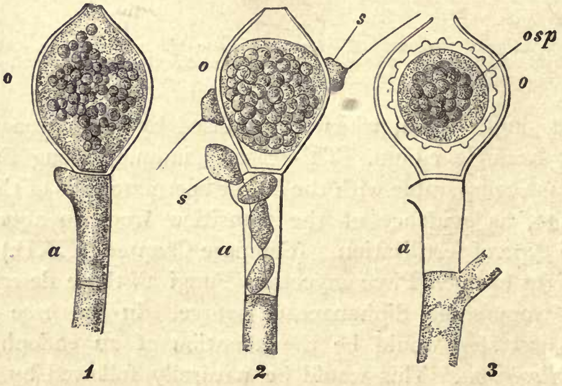


FIG. 358.

Monoblepharis sphaerica. End of a filament with terminal oogonium (*o*) and an antheridium (*a*). 1, before formation of the gametes. 2, spermatozoids (*s*) escaping and approaching the opening of the oogonium. 3, *osp*, ripe zygote and an empty antheridium. (After Cornu. ×800.) (From Strasburger.)

free spermatozoids, but transfers a single gamete by a tube, as in the higher land-living Plants. The oogonium retains its character as in *Vaucheria*. All these presumed changes are biologically likely to occur. Such considerations justify the recognition of Fungi included among the Oosporeae as of probable Siphonaceous origin, from types already advanced in their sexuality as far as *Vaucheria* is.

PHYCOMYCETES.—(*b*) ZYGOMYCETES.

The Mucors.

The Zygomycetes include many common Moulds. They are mostly saprophytes, though some of them are parasites not only on other plants and animals, but even on one another. They are characterised first by their coarse non-septate hyphae, but more particularly by the manner of their sexual reproduction, which results from the fusion of two similar, multinucleate branch-endings, to form a single large resting-spore, or *zygo-spore*. The chief representatives are the Mucors (Mucorineae) found on decaying organic matter in moist circumstances. If moist bread, horse-dung, brewer's grains, or other organic substances be kept warm for a day or two under a bell-glass, Mucorineous Moulds will almost certainly appear. They are often of considerable stature. *Phycomyces nitens*, which comes commonly on brewer's grains, may be several inches in height, the coarse *sporangiophores* ending in *sporangia* easily seen with the naked eye.

Another common type is *Empusa muscae* (Entomophthorineae), which lives parasitically on the House Fly. In autumn the infected flies become sluggish, and finally resting on a window pane, or elsewhere, they appear as though surrounded by a white halo. This is formed by the conidia thrown off to a distance by the conidiophores, which project from the body of the fly killed by the fungus in its vegetative stage. Thus, while most of the Fungi of this group are saprophytes, some may be parasitic, even on animals.

If the sporangiophores of *Mucor* or *Phycomyces* be followed to their base, they are found to arise from finer filaments forming a profusely branched *mycelium*, which traverses the substratum. A good idea of its nature is obtained by culture from the spore on a glass surface (Fig. 359). It is then seen how, starting from the spore as a centre, the mycelium may radiate outwards, with successively finer branches of its non-septate tubes. Each of the thick upright *sporangiophores* bears one sporangium on its end, which when ripe consists of a brittle external wall surrounding many spores embedded in a mucilaginous matrix, while centrally is a large columella (Fig. 359, *A*). It is difficult to see this structure satisfactorily in ripe sporangia mounted in water, owing to the swelling of the mucilaginous matrix, which

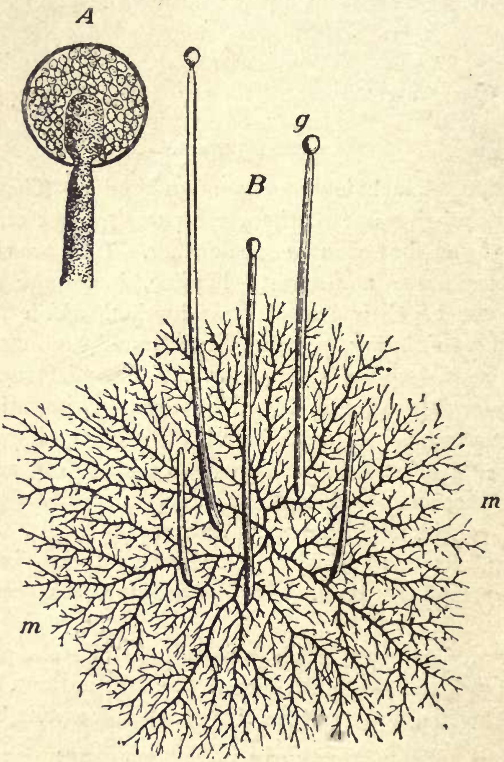


FIG. 359.

A plant of *Mucor*, showing the mycelium of branched hyphae (*m*) and sporangia (*g*). *A* is a single sporangium more highly magnified, containing spores. (After Brefeld.)

bursts the wall and scatters the spores (Fig. 360). Their dissemination is thus through the assistance of water, not in the dry and dusty state common for most Fungi.

Though this is the case for the typical Mucors, there are many Mucorineous Fungi in which the dissemination of spores is through the air. They are found among those smaller forms which live parasitically on the larger Mucors, and frequently appear upon old cultures of these as flocculent growths attached by suckers to their sporangiophores (*Chaetocladium*, *Piptocephalis*). In these parasites the sporangiophores are profusely branched, and they bear many unicellular, conidium-like bodies, easily detached, and carried by the wind. That they are really sporangia of very reduced form is indicated by intermediate types, with minute sporangia, which contain a few spores. Even *Mucor* itself, when starved, may produce such small sporangia, which show how the still simpler condition may arise. The family thus illustrates a transition from water-dispersal, by spores produced internally in few large sporangia, to dispersal through the air of sporangia reduced to a single cell, and produced in larger numbers. The latter may be held as a derivative condition.

A very peculiar mode of dispersal is by forcible projection of the whole sporangial head. This is seen in *Pilobolus*, whence its name. The sporangium is constructed like that of *Mucor*; but at ripeness it breaks away from the

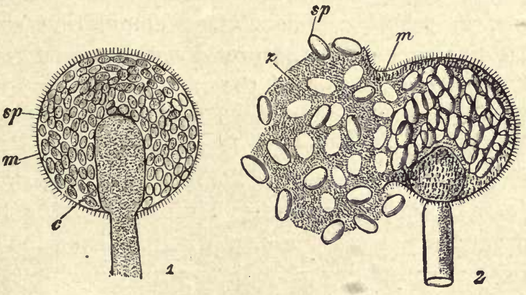


FIG. 360.

1, *Mucor mucedo*, a sporangium in optical longitudinal section. *c*=columella. *m*=wall of sporangium. *sp*=spores. 2. *Mucor mucilagineus*, a sporangium shedding its spores; the wall (*m*) is ruptured, and the mucilaginous matrix (*z*) is greatly swollen. (After Brefeld. 1 × 225; 2 × 300, after v. Tavel.) (From Strasburger.)

stalk, which has become turgid with sap under osmotic pressure. By the principle of the squirt this fluid is thrown out to a distance of some inches, carrying with it the sporangial head. A similar projection happens in *Empusa*, but here it is only a single conidium that is discharged, which, adhering to any solid body, causes the halo previously mentioned. There is thus a considerable variety in the methods of dissemination in the Zygomycetes.

The spores of many of the Mucorineae contain more than one nucleus. There are said to be two in *Pilobolus*, and many in *Sporodinia*. In the latter, which grows parasitically on large saprophytic species of *Boletus*, the sporangial head is first shut off by a septum: this becomes convex, and forms the central columella. The large poly-nucleate mass of protoplasm filling the head then undergoes cleavage into a number of parts, each containing several nuclei. These rounding themselves off form the spores. Such cleavage of the contents of the sporangium is the typical method of formation of spores in the Mucorini. The final result is the same in all: viz. germination under favourable circumstances to form a new non-septate, and poly-nucleate mycelium.

The mycelium of *Mucor* may vary in its mode of growth according to the medium. If it be submerged in fluid it shows the *Oidium*-condition, where, dividing into short lengths, each of these may increase by a process of budding not unlike a yeast. Or again, if the conditions are unfavourable, the starved mycelium may divide transversely, and the portions become thick-walled, as *Chlamydospores*, a state reminiscent of the behaviour of *Vaucheria geminata* under like conditions (p. 398). When the circumstances are again favourable, either of these states may pass over into the normal mycelium again.

The chief alternative mode of propagation is, however, by the production of *Zygospores*. In many Mucorineae this is normally a rare event, in others common. One dominating circumstance, the fact of a difference of the nature of sex, has only recently been ascertained as an explanation of the rarity. The essential feature is the coalescence of the ends of two equal club-shaped hyphae to form a single fusion-body, which is the zygospore. Two hyphal branches, either of the same mycelium (*Sporodinia*), or of distinct mycelia (*Mucor stolonifer*, and other Mucors), growing towards one another, meet at their apices (Fig. 345, p. 410). From the end of each a conjugating cell containing protoplasm with many nuclei is cut off by a transverse septum. Their apices flatten, and the cells fuse, the wall separating them being absorbed. They may be called "coenogametes," and the result is a "coenozygote," since many nuclei are involved instead of a single one in each. The large resulting protoplast is stored with nutritive material, while the outer wall thickens, often forming characteristic bosses externally (Fig. 345, p. 410). In this condition the zygospore may undergo a period of rest, and is resistant to unfavourable conditions. But suitable conditions induce germination, and they determine what follows. Sometimes there is a formation of a vegetative mycelium, sometimes an immediate formation of a sporangium, as in Fig. 345, 5.

A remarkable fact is the occurrence in some Mucorineae of "*Azygospores*," that is, bodies that resemble zygospores in their structure and covering, but are produced without any fusion.

According to their power and readiness for conjugation the Mucorineae have been divided into two groups. The *Homothallic*, which form zygospores on two branches of the same mycelium, so that by sowing a single spore zygospores may be obtained. This is seen in *Sporodinia*, in which the zygospores may often be obtained in the open in autumn. Others are called *Heterothallic*, where the presence of two individuals of two different types are necessary for the production of zygospores (*Rhizopus*, *Mucor*, *Phycomyces*). These types are distinguished as + and −, rather than as male and female, because there is no recognisable difference of form or structure, but only of function. If either be cultivated pure, and apart, the mycelium bears no zygospores. But if cultures of the + and − types be started apart and meet, a profuse formation of zygospores appears along the line of junction (Fig. 361). The behaviour is thus similar to that seen in unisexual plants. Functionally the Homothallic may be compared with the Monoecious condition, the Heterothallic with the Dioecious state. But these comparisons must not be pressed too closely. The facts thus disclosed give a ready explanation of the rarity of zygospores in certain cases, and their frequency in others.

The facts of the life-history in the Zygomycetes show a less direct dependence of these plants on external fluid water than in the Oomycetes, for there are no zoöspores motile by cilia. Still the dissemination of the spores in the Mucors is through swelling of mucilage in water, or ejection where fluid pressure gives the propulsive power.

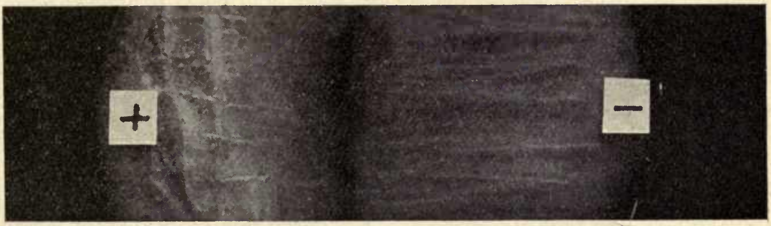


FIG. 361.

Result of a plate-culture of the heterothallic *Mucor hiemalis*, made by Mr. Drummond. + and − strains were started on opposite sides of the plate. The dark line transversely between these shows where the cultures meet, and the zygospores were formed. (½ natural size.)

The series with branched sporangiophores, and wind-borne conidia is a step still further away from dependence upon the water-medium. Comparison suggests for the more primitive sporangia such as *Mucor* an origin from a sporangium like that of a Siphonaceous Alga. The loss of motility of the spores which is involved is readily understood in organisms living in moist air in place of water.

The formation of zygospores presents the unusual condition of the fusion not of single cells as in the Conjugatae, but of coeno-gametes to form a coeno-zygote. There is reason to believe that numerous nuclear fusions take place: in fact that the formation of the zygospore is a fusion of gametangia, rather than of single gametes. If two gametangia, like those of *Codium* or *Bryopsis*, were to fuse as a whole, in place of opening and shedding their gametes to fuse singly, the result would be very like what is seen in the Mucorineae. Provisionally this seems the best interpretation of the facts. Even the Azygospores may receive a similar interpretation. In some

Algae, where sexual evolution is incomplete, the gametes can germinate without fusion. If the whole gametangium could do this, the result would be what is seen in the azygospores.

Comparing the Phycomycetes as a whole with the Siphonaceous Algae, the Zygosporeae would be referable in origin to the more primitive Siphoneae, in which the differentiation of sex was less advanced. The Oosporeae, on the other hand, would be referable to more advanced types, in which sexual differentiation extended to the gametangia themselves. Probably the Zygomycetes and Oomycetes represent two distinct lines of evolution, of which the Oomycetes started subsequently to the advance n sexual differentiation.

CHAPTER XXVIII.

EU-MYCETES.—(*a*) ASCOMYCETES.

THE Fungi belonging to the Ascomycetes, the first sub-class of the septate Eu-mycetes, are very various in habit. Many are parasites, often on leaves and stems of Flowering Plants: for instance the Mildews, such as *Sphaerotheca*. Others are saprophytes, such as the small and prevalent Moulds, *Aspergillus* and *Penicillium*. Others again form large fruiting bodies, such as those of *Peziza*, or the edible Truffle (*Tuber*), or the Morel (*Morchella*). Some are parasitic on animals, as in the case of *Cordyceps*, which invades caterpillars and the larvae of Cockroaches. The Ascomycetes are thus not only a large but a very varied group of Fungi.

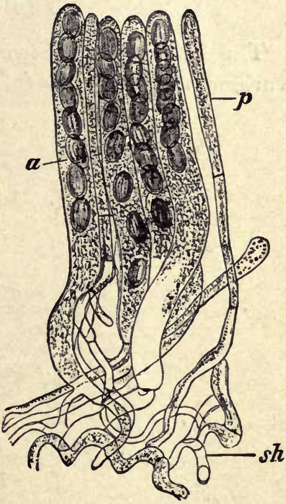


FIG. 362.

Portion of the hymenium of the Morel (*Morchella esculenta*). *a*=asci. *p*=paraphyses. *sh*=sub-hymenial tissue. (×240.) (After Strasburger.)

Their characteristic feature is a club-shaped or oval body, the *Ascus*, within which *Asco-spores* usually to the number of eight are contained (Fig. 362). Such asci may occasionally be produced singly in very simple forms, such as *Sphaerotheca*; but they are commonly associated together in large numbers, in fruit-bodies of various form. In many cases the development of the asci has been found to follow on the formation of *sexual organs*, of which the female is a *carpogonium*, sometimes with a receptive *trichogyne*, as in the Red Seaweeds. The ascospores may therefore be held to be of the nature of post-sexual *carpospores*. In other cases the sexual organs have not been found, and there is reason to believe that normal sexuality has passed into abeyance in many of these parasitic and saprophytic plants, though the asci still remain as morphologically representing the products of the carpogonium. In most of these Fungi there is also propagation by means of minute *conidia*, which are not sexually produced. They are borne on *conidiophores*, which are various and characteristic in form.

The young unicellular ascus has originally two nuclei, which are held to be derived from the paired but not yet fused nuclei of a preceding fertilisation. These nuclei fuse as the development proceeds, and the resulting nucleus then divides into two, four, and usually eight (Fig. 362). These divisions are associated with a process of reduction. Each nucleus then becomes a centre of free-cell-formation : an area of cytoplasm round each is delimited by a cell-wall, leaving over a residuum of cytoplasm which embeds the spores till ripeness. The spores are liberated either by forcible ejection from the ascus, or frequently by drying up, and rupture of its wall.

THE MILDEWS (*Erysipheae*).

The Mildews are Ascomycetous Fungi, parasitic on the leaves of various plants. They take their name from the fact that the patches

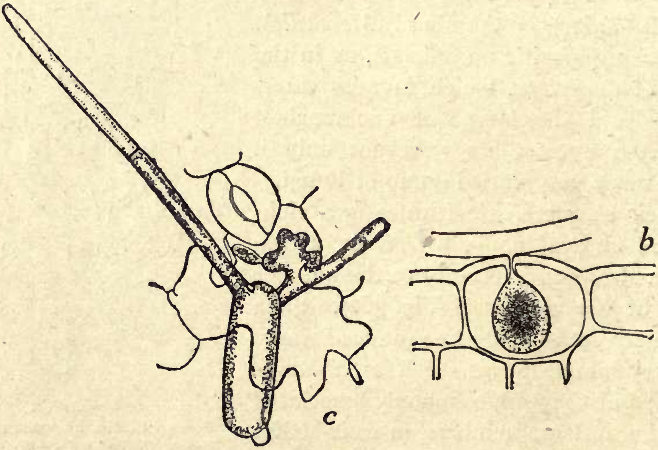


FIG. 363.
c=a germinating conidium of an *Erysiphe*, showing how the young germ-tube at once attaches itself by a haustorium to the epidermis. *b*=a haustorium in section. (After De Bary, highly magnified.) (From Marshall Ward.)

of the disease appear white and floury, owing to the formation of their *conidia*, produced from a cobweb-like mycelium, which grows on the outside of the infected leaf. Its hyphae are attached to the leaf by *haustoria*, which penetrate the outer walls of the epidermal cells, the connection being established immediately on the germination of the infecting conidium (Fig. 363). As the season progresses small dark specks make their appearance, large enough to be seen with the naked eye. These are the fruits, or *perithecia*, each containing one or more *asci*. In damp weather these parasites develop quickly, a fact that has drawn almost superstitious attention to them. A very common example is seen in *Podosphaera clandestina*, which infests the leaves of the Hawthorn in any warm and wet autumn.

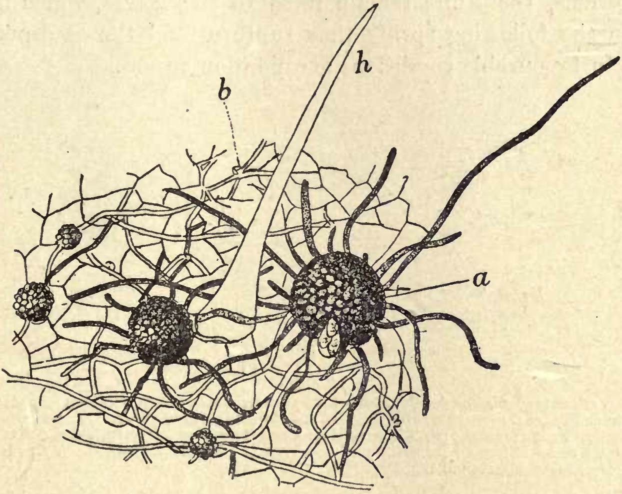


FIG. 364.
Piece of epidermis of Hop, showing mycelium (*b*) and perithecia (*a*) of the Hop-mildew on its surface. *h* is a large hair. At (*b*) the first beginnings of a perithecium. Magnified. (After Marshall Ward.)

A still simpler one, *Sphaerotheca castagnei*, causes a disease on the cultivated Hop, though it may occur also on many other plants. The effect of Mildews on the infected plant is that the diseased areas take a pale colour, nourishment being withdrawn from them. But there is no malformation.

After the Hop-Mildew has established itself, and formed a branched, septate mycelium, certain hyphae grow vertically upwards from the leaf-surface without branching: they segment transversely into short lengths, which become detached in basipetal series as *conidia*, easily removed when ripe by a breath of air. They will germinate on a moist leaf, and cause new infections during the summer (Fig. 363). But later the fruit-bodies (*perithecia*) appear, which provide for the winter's rest (Fig. 364). They arise where the branched hyphae cross or touch one another. Two short branches grow erect, and a uni-nucleate cell is shut off from the end of each. One which is larger is recognised as the *oogonium*, the other which is smaller is the *antheridium*. They fuse, and the nucleus of the latter passes into the former, which then becomes surrounded by an investment of upgrowing filaments, forming an outer shell to the fruit. Meanwhile the oogonium divides into a row of cells, and the terminal cell forms the *single ascus*, with eight *ascospores* (Fig. 365). Protected by the outer shell, and attached by long filaments which grow out from their surface, the fruits remain fixed to the leaves, which fall and rot. In the following spring they rupture, and the ascospores are shed. In favourable conditions germination ensues.

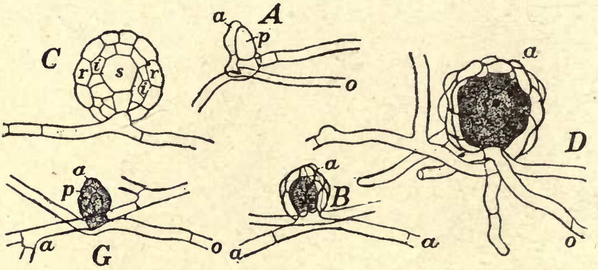


FIG. 365.

Various stages in the development of the perithecium of the Hop-mildew, showing the contact of the two short branches (*A*), one of which (*p*) gradually becomes invested by enveloping branches (*B*). The envelope forms the wall of the perithecium, and the single ascus is formed from the enclosed branch. Highly magnified. (After De Bary.) (From Marshall Ward.)

This is probably the simplest type of Ascomycetous fruit. In *Erysiphe* and others hyphae are produced from the female organ, and they bear *numerous asci*. Such developments lead on to the more complex fruit-bodies of the larger Ascomycetous Fungi.

MOULDS (*Plectascineae*).

If bread, or any organic body such as leather or jam, be kept in a closed damp space, for instance under a bell-glass, or in a damp cupboard, it will become mouldy. This is due to the germination upon it of air-borne spores of Moulds that are always present about the dwellings of man. These Moulds at first form isolated patches on the bread, which then run together, covering the whole surface, and also penetrating inwards. There are many different Moulds that may thus appear, and they grow mixed together, or they may be segregated into distinct, purer patches. Where this occurs the two commonest are readily distinguished by their stature and colour. Low-growing, velvety, blue-green patches are *Penicillium crustaceum*; coarser, olive-green patches, with mop-like heads, of size visible to the naked eye, are *Aspergillus* (*Eurotium*) *herbariorum*. As the patches of the latter grow older, minute yellow specks may appear upon them: these are the *Eurotium*-fruits, a stage originally described as a distinct fungus. A breath will carry away the numerous *conidia* from such a culture in a dense cloud. They form part of the ordinary dust of dwellings, and this accounts for the constant appearance of

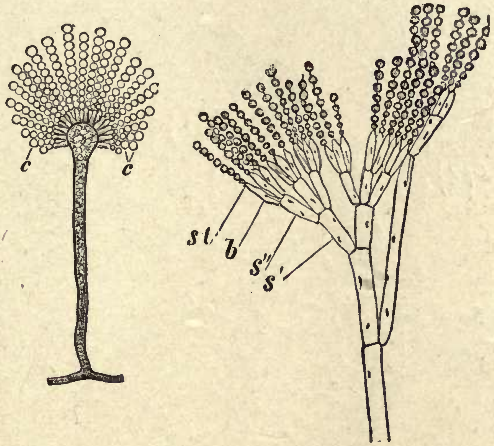


FIG. 366.
Conidiophores of *Aspergillus herbariorum* (to the left) and of *Penicillium crustaceum* (to the right.) (From Strasburger.) Highly magnified.

the Moulds on organic substrata where the conditions are favourable to their growth, as in the moist air in a close cupboard, or under a bell-jar.

If a sample of *Aspergillus* be taken, the branched and septate mycelium is seen to ramify over and penetrate into the organic substratum, deriving nourishment till able to propagate. Stout branches then rise upright as *conidiophores*, which swell upwards into a spherical head. On this numerous conical *sterigmata* bud forth, each giving rise to a chain of *conidia*, formed in basipetal succession. The oldest is distal, and successively others are abstricted off: an arrangement which provides for the due nourishment of each, and the ready removal of those that are mature by any breath of air; for these minute polynucleate bodies are very lightly attached (Fig. 366). They germinate readily in water or damp air, and the mycelium permeates any nutritive medium; thus they serve for the quick spread of the Mould. The corresponding conidiophores of *Penicillium* are constructed on a similar plan, but are much smaller. Instead of bearing a mop-like head, they are repeatedly branched, giving them a brush-like appearance, while from the end of each branch a chain of conidia is abstricted, as before (Fig. 366).

The alternative method of propagation follows in *Aspergillus* on a rise of temperature, and results in those yellow fruits originally

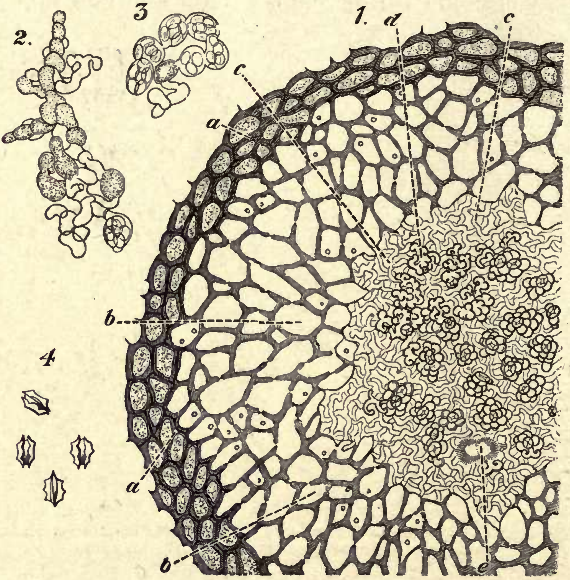


FIG. 367.

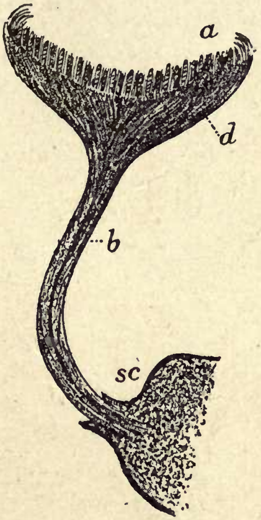
1, Section through part of a fruit of *Penicillium*; *a*, *b*, pseudo-parenchymatous covering; *d*=ascogenous hyphae. 2, 3, ascogenous hyphae with asci, more highly magnified. 4, ascospores. (After Brefeld.)

described under the name of *Eurotium*. When ripe each contains numerous asci, and spores. Similar fruits are formed also in *Penicillium*, but more rarely. The development originates in either case from a spiral or twisted *carpogonium*, which is associated with an *antheridium*. As in *Sphaerotheca* these sexual organs become enveloped in a pseudo-parenchymatous covering, derived from the mycelium that bears them. The carpogonium divides into a number of cells, from which strong hyphae arise. These are nourished by the surrounding tissue, and produce the numerous oval *asci*, each with eight *ascospores*. In *Penicillium* the structure of the fruit-body is more complicated than in *Aspergillus* (Fig. 367). In either case the result at ripeness is that the fruit appears as a dry spherical sac, filled with ascospores set free by the disappearance of the ascus-walls, and of the nutritive tissues that embedded them. On germination the ascospores form a new mycelium. (Fig. 367, 2, 3, 4.)

In *Aspergillus* both the antheridial and carpogonial cells are multinucleate, and it appears that sometimes a normal sexual fusion takes place. But in others the antheridium degenerates, and sexual fusion is replaced by a fusion of ascogonial nuclei in pairs. Thus *Aspergillus* illustrates that degradation of sexuality, evidence of which is common among the Fungi.

The type of life-history seen in these simple Mildews and Moulds is common for other Ascomycetes, though it may be worked out with greater complication. But in many of them the sexual organs are so degraded that they, or their

A



B

FIG. 368.

A, a sclerotium of *Peziza*, which has germinated and given rise to numerous trumpet-shaped discs. *B*, section through such a sclerotium (*sc*), and the *Peziza* disc (*d*) to which it has given rise. *b*=stalk. *a*=asci. Magnified and slightly diagrammatic. (From Marshall Ward.)

equivalents, if present, have hitherto escaped observation. There is normally an alternation of generations, the critical points of which are the sexual fusion in the carpogonium, and the reduction which precedes the formation of the ascospores. The stage of the ascogenous hyphae, which intervenes between these events may be regarded as a *diploid sporophyte*. The rest is held to be the *haploid gametophyte*, which is liable to indefinite repetition by means of conidia. The fruit-body is then a composite structure, consisting essentially of the ascogenous hyphae, constituting the sporophyte, which is enveloped in a covering derived from the mycelial gametophyte. The nearest analogies are with the fruiting bodies of the Red Seaweeds.

Both the mycelial and the fruiting stages of Ascomycetous Fungi are subject to modifications according to habit and circumstance, and either may attain large size. The mycelium may, by repeated branching and knotting together of its hyphae, form dense masses stored with nutritive material, hard and dark coloured, called *sclerotia*. When the rest of the mycelium is killed off by dry or cold weather

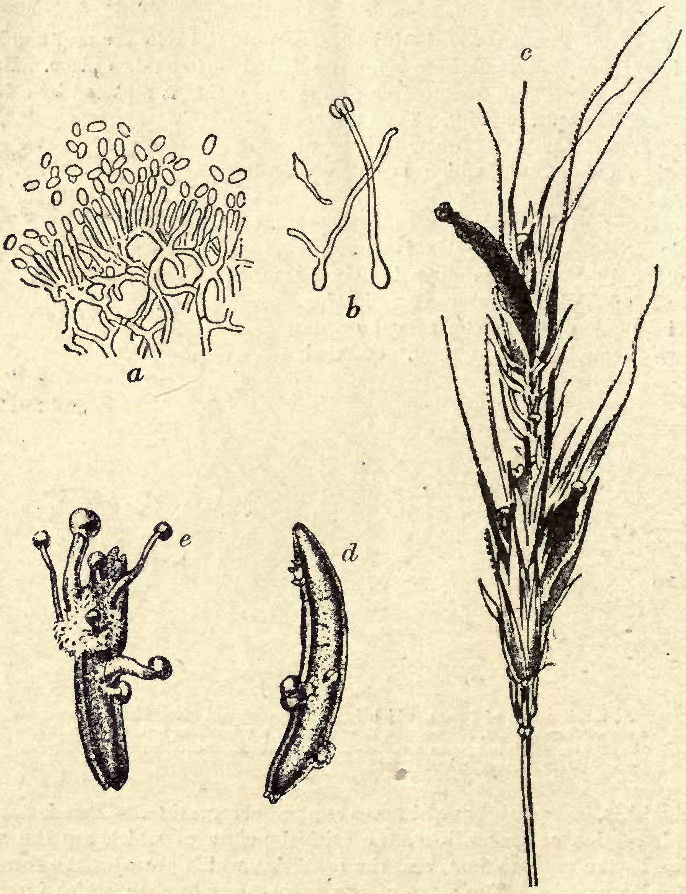


FIG. 369.
a, *b*=conidial stage of *Claviceps*, developed in the flower of Rye. *c*=sclerotia replacing the grains of the ear of Rye. *d*, *e*=germination of the sclerotia in spring. See Text. (After Tulasne.) (From Marshall Ward.)

these remain uninjured, and may germinate, forming at first fresh superficial mycelium and conidia; but, later on, outgrowths may spring directly from them, as in some species of *Peziza*, which bear broad disc-like fruits. Those Ascomycetes which have such flat open fruits are ranked as *Discomycetes* (Fig. 368). The most notorious sclerotia are those of *Claviceps purpurea*, the Ergot of Rye, a fungus which causes a disease on Rye-crops. The fungus attacks the ovaries of the Rye and other Grasses at the flowering period, spreading over them and causing the condition known as "Honey-Dew." This is the conidial stage, and it is spread from plant to plant by insects, which are attracted by a sugary secretion in which the conidia float (Fig. 369, *a*, *b*; also Fig. 341, p. 406). But the effect becomes more apparent as the crop ripens, for in place of the normal grains long curved bodies project from the ear (Fig. 369, *c*). These are the *sclerotia* of the fungus, which fall off at the time of ripening of the grain. They are the commercial source of supply of a useful drug. In this resting stage the winter is passed. In spring the sclerotia germinate, forming numerous pinhead-like growths, which bear the flask-shaped perithecia characteristic of the large group of the *Pyrenomycetes* (Fig. 369, *d*, *e*). Finally in these the asci and thread-like ascospores are matured at about the time when the Grasses flower. It has been proved experimentally that hyphae from the germinating spores invade the Grass-flowers, causing the development of the conidial stage again. The

FIG. 370.

Morchella esculenta, the fruiting body of the Morel. The convoluted folds of surface are covered by the hymenial layer, bearing asci. (½ nat. size.) (After Strasburger.)

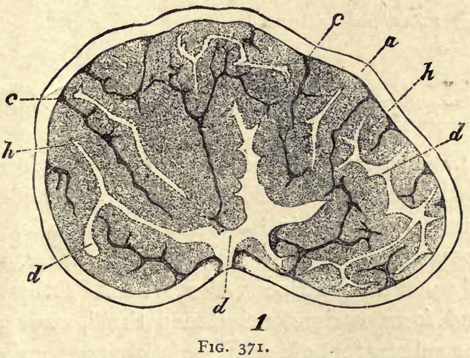


FIG. 371.

Tuber rufum: a Truffle. The fructification in vertical section (×5). *a*=cortex. *c*=dark veins of compact hyphae. *d*=air-containing tissue. *h*=ascogenous hyphae, with numerous asci. (After Tulasne; from Strasburger.)

life-history is here essentially the same as before, but with the addition of the resting sclerotium.

The fruit-bodies are very complex in some of the larger saprophytic Ascomycetes. An extreme case is seen in the edible Morel (*Morchella esculenta*), in which the external hymenial surface is convoluted so as to accommodate a vast number of asci. It is possible to refer this to an elaboration of the Discomycetous type, as it is seen in *Peziza* (Fig. 370). But in the Truffle (*Tuber*) the equally numerous asci are borne internally, in the large underground tuberous fruit (Fig. 371).

ASCO-LICHENES

There is a series of Ascomycetous Fungi which live in symbiotic relation with Algae, and thus constitute compound bodies which are called *Lichens*. The physiological relation of the two distinct organisms is not unlike that of the Fungus and Host-plant in mycorhiza, but there is here no intra-cellular digestion

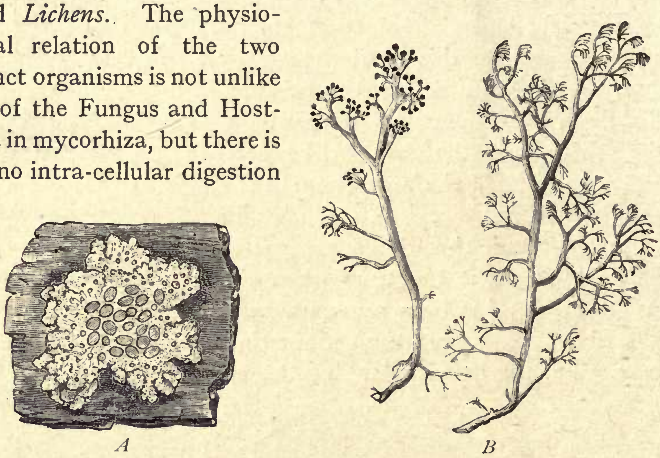


FIG. 372.
A = *Xanthoria* (*Parmelia*) *parietina*, the common foliaceous yellow Lichen. *B* = *Cladonia rangifera*, a fruticose Lichen. Both bear ascus-fruits, and are shown natural size. (After Strasburger.)

(Chapter XI.). The Lichens are very various in form. In simple cases they may be filamentous, as in *Ephebe*, which is like a filamentous Alga with a fungus growing in its mucilaginous walls. Some appear as flat gelatinous thalli, readily swelling with water, as in *Collema*, which is based upon the gelatinous Alga, *Nostoc*. Others are more firm in texture, and form variously flattened thalli, more or less closely attached to the substratum of rocks, roofs, or tree-trunks, etc. Others again are erect or pendulous, and often branched, rising freely from their base of attachment. In texture they are brittle when dry, but more or less leathery when moist, and they vary greatly in colour from grey to more vivid yellow, or even red. They are curiously susceptible to impurities in the air, and are absent from urban areas (Fig. 372).

Their structure shows two distinct constituents. Certain cells have Algal characters, and often closely resemble Algae known in the free state; they contain chlorophyll or some related colouring matter, and are photo-synthetic. They are distributed variously in the thallus, often in a definite *gonidial layer*. These cells are closely invested by the fungal constituent, which is composed of

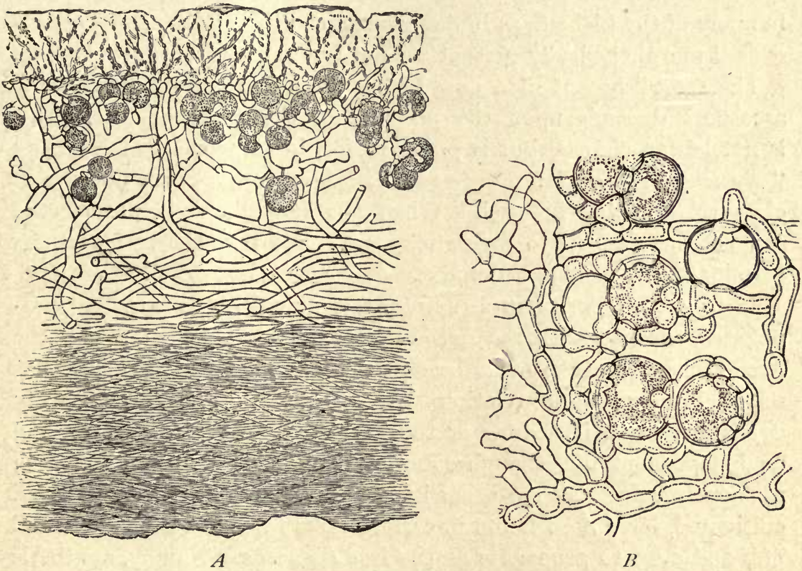


FIG. 373.

Cladonia furcata. *A* = vertical section of the thallus showing the inverted gonidial layer below the cortical sheath (× 330). *B* = part of the same highly magnified, to show the mode of attachment of the hyphae to the gonidia (× 950). (After Bornet.)

septate and branched hyphae, twigs of which enwrap the Algal cells, establishing intimate physiological relations (Fig. 373). Not only does this dual organism flourish, but it may also propagate as such. In wet weather many Lichens are covered by a mealy powder, extruded from within. Examination shows that it is composed of *soredia*, which are bodies containing both constituents of the thallus; and each soredium is thus able to grow directly into a new Lichen.

The fruiting bodies of the Lichens are, however, produced from the Fungal constituent only, and most of them closely resemble those of Disco-mycetous and Pyreno-mycetous Fungi in form and construction (Fig. 372, *A*). In the Iceland Moss (*Cetraria Islandica*), which is official, the fruits appear as marginal discs. When cut vertically they show a superficial *hymenium*, with numerous asci arranged as in *Peziza* (compare Fig. 362, p. 429). Male sexual organs are sometimes borne, as minute, non-motile bodies (*spermatia*), which are produced in flask-shaped *spermogonia*, contained in the marginal teeth of the thallus. Female organs have been seen in some of the Lichens (*Collema*, etc.) to have the form of a coiled *carpogonium* with a receptive *trichogyne* that projects to receive the non-motile spermatium, as in the Red Seaweeds. But it seems probable that in many of the Lichens, as in many advanced Fungi, the sexual organs even if morphologically present are not functional.

The establishment of a new Lichen from the germination of the ascospore depends upon the presence of the Algal partner. This is not left to chance, but is provided for, in some cases at least, by "*hymenial gonidia*": these are small Algal cells which develop in close relation to the asci. When the fungal spores are ejected some of these adhere to their sticky walls, and thus the two partners germinate together from the first.

The close similarity in structure, nutritional behaviour, and propagative method with the Ascomycetes makes it probable that the Asco-Lichens arose from a branch of the Ascomycetes, which has adopted a symbiotic relation with Algae, and become actually dependent upon it. None of the Lichen-Fungi are known to lead an independent life, though some of them have been cultivated in nutrient media. On the other hand the Algal cells, if liberated and cultivated, have been found in certain cases to continue their normal life, and even to propagate as the free Algae do. Finally, synthetic experiments have succeeded in building up a Lichen from its two constituents when grown together. The proof that the Lichen consists of a coalition of two organisms living in symbiotic relation seems thus complete. That the symbiosis is a mutual advantage is clear from the healthy growth. It may be held that the Algae contribute fresh organic substance by photo-synthesis, while the Fungus supplies water and soluble salts, which it is specially able to extract and convey.

CHAPTER XXIX.

EU-MYCETES.—(*b*) BASIDIOMYCETES.

THE Basidiomycetes form the second sub-class of the septate Eu-mycetes. They include most of the large Fungi, such as the Mushrooms, Toad-stools, Shelf-Fungi, and Puff-Balls. These are almost all saprophytes. But the Basidio-mycetes also include the Rusts and Smuts, which are parasitic forms causing disease. Some of these are the most injurious pests to cereal crops, such as the Rust of Wheat, or the Smut of Oats. Some Basidiomycetes also take part in the formation of certain types of Lichens. They are thus very varied in their habit, and include many familiar objects. The characteristic feature is the *Basidium*, which takes a place in the life-cycle corresponding to the ascus in the Ascomycetes; for in both of them there is nuclear reduction, and both pro-duce post-sexual *Carpospores*. But while in the ascus they are formed internally (Fig. 362, p. 429), in the basidium they are borne externally (Fig. 374).

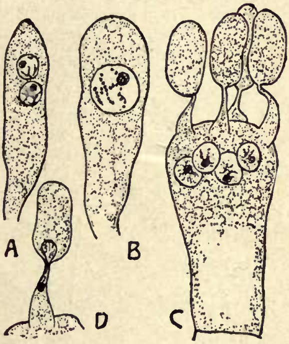


FIG. 374.

Honey Agaric (*Armillaria mellea*). *A*, young basidium with two primary nuclei. *B*, after fusion of the two nuclei. *C*=a basidium of *Hypholoma appendiculatum* before the four nuclei derived from the secondary nucleus of the basidium have passed into the four basidiospores. *D*=passage of a nucleus into the basidiospore. (After Ruhland.) (From Strasburger.)

In the Basidiomycetes normal sexuality has not been shown to exist, while it is only in the Uredineae or Rusts that organs are found which, though no longer functional as such, are held to be of the nature of sexual organs. This would indicate that the Uredineae are relatively primitive types of the Basidiomycetes. It may be held as probable that all these Fungi were derived from a sexually reproducing ancestry; but that the sexuality is in abeyance in the more advanced parasites and saprophytes, while vestiges of it remain in the more primitive Rusts.

The *basidium* resembles the ascus in containing *two nuclei* when young. As in the ascus these first fuse with one another, and then follows division, first into two then into four, which is accompanied by *nuclear reduction*. In the more primitive types (Uredineae, Tremellini), the basidium divides after the fusion: in the Rusts it appears as a short mycelium (promycelium) from which four cells are partitioned off; each of these puts out a short beak, or *sterigma*, and bears a *carpospore* (Fig. below, p. 446). In the more advanced types, such as the Toad-stools and Puff-balls, the basidium does not divide into distinct cells; but sterigmata are formed, and each produces a basidiospore or carpospore, which behaves in the same way as in the Uredineae. The difference is that the basidium remains undivided. (Fig. 374.)

UREDINEAE.—RUST-FUNGI.

The Rust-Fungi are very prevalent parasites on the shoots of many plants, and as their mycelium lives in the intercellular spaces of the infected areas, and draws nourishment from the cells, the host-plant suffers, though it struggles on without being killed. If the host be perennial, the fall of the leaf, or dying down of the aerial shoot, rids it temporarily of its enemy, and the parasite has to make a new infection in the succeeding season. It is only occasionally, as in *Gymnosporangium* on the Juniper, that the fungus perennates in the host. A very large number of Rust-Fungi are known, and they show a high degree of specialisation in their parasitism, being mostly restricted to certain genera, or even species of host; while in not a few cases their elaborate life-cycle is completed by stages of growth upon two distinct and successive hosts. This is described as *Heteroecism*. The name Rust is derived from the fact that the spores produced by them in summer are of the

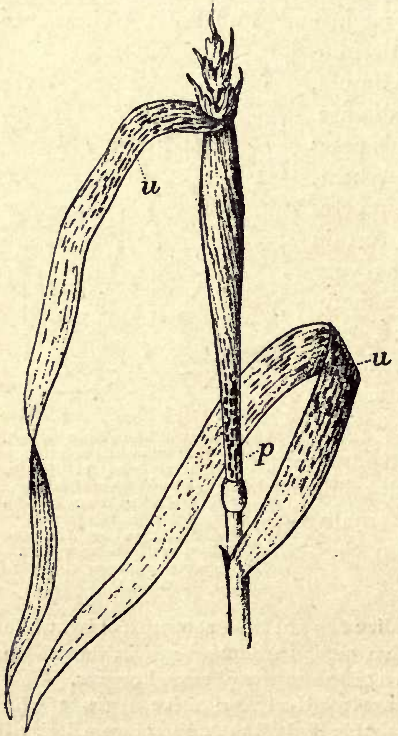


FIG. 375.
Upper portion of a stalk of Wheat, with groups of Uredo-spores (*u*) on the leaves, and of Teleuto-spores (*p*) on the fast-ripening leaf-sheath and straw. (After Marshall Ward.)

colour of rust of iron. They are found in such quantity as to attract public attention, and this has provided the name.

The most familiar example, as it is also economically the most important, is the Rust of Wheat, *Puccinia graminis.* In June and July the green leaves of the Wheat are often seen to lose their colour (Fig. 375). Yellow patches appear between the veins, and run together into lines that follow the softer mesophyll. The epidermis bursts, and innumerable orange spores are set free, which are easily carried as dust by the wind. These are the *Uredo-* or *Summer-spores* of the Rust. A part of a field thus diseased is a centre of infection, and the fungus may often be seen to spread from it down the prevailing

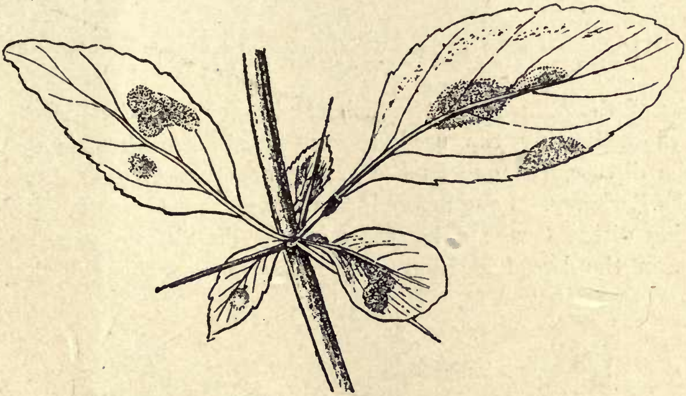


FIG. 376.
Part of shoot of Barberry with leaves attacked by *Aecidium Berberidis*, which forms yellow cushions on the leaf-blades and stalks. (After Marshall Ward.)

wind. This production of spores, which represents so much material robbed from the developing crop, may continue till autumn; but gradually the patches of disease change in colour to a dark purple-brown. This is due to the formation in them of a new kind of spore, the *Winter-* or *Teleuto-spore*, which is firmly attached to the straw, and dies down with it, or is removed with the crop. These spores retain their vitality till the next spring, when they germinate (Fig. 375).

The result of their germination has been shown experimentally to be the infection of the leaves of the Barberry plant, and the production of a second stage, which appears as red or yellow blotches, thicker than the healthy parts of the leaves that bear them: small dark spots open on the upper surface (*spermogonia*), and numerous widely gaping cups (*aecidia*) are clustered together on the lower surface. This stage was first described as "Cluster-Cups," and regarded as a distinct fungal disease under the name of *Aecidium berberidis* (Fig. 376). But it is now known that the spores produced by the cups are able on germination to cause a new infection of the

FIG. 377.
Longitudinal section of a leaf of Wheat, showing a tuft of Uredo-spores bursting through the epidermis. Highly magnified. (After Marshall Ward.)

leaves of the Wheat plant, which results again in the growth of a mycelium bearing the uredo-spores. There are thus two stages of the disease, the one on the Wheat or other Grasses, the other on the Barberry. Long before it was proved that these two different-looking diseases were only stages in one life-history, a connection between the two had been suspected. It was thought that the

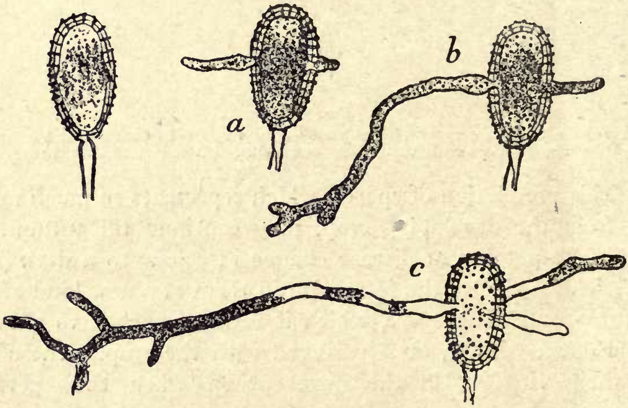


FIG. 378.
Germinating Uredo-spores, showing various stages of development of the germ-tubes, *a*, *b*, *c*. Very highly magnified. (After Marshall Ward.)

Barberry was in some way injurious to Wheat. But it was not till late in the nineteenth century that the cycle was completely demonstrated. A similar heteroecismal life is now known for about fifty species of Rusts. One of the commonest is *Puccinia caricis*, of which the uredo-spores and teleuto-spores are on leaves of species of *Carex*, and the aecidium-stage on the common Nettle, causing contorted swellings upon its stem and leaves. Thus the Rust of Wheat is an example of a life-history that is not uncommon.

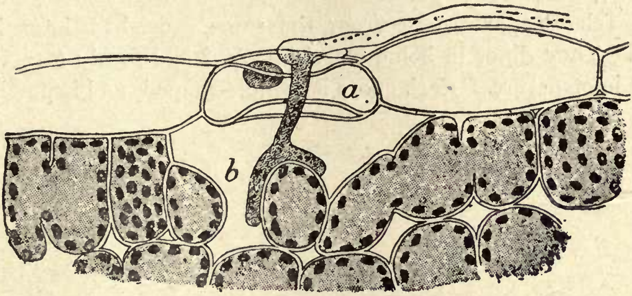


Fig. 379.
Longitudinal section of a leaf of Wheat, showing a germ-tube of a *Uredo*-spore passing through a stoma (*a*) into the intercellular space (*b*). Very highly magnified. (After Marshall Ward.)

Sections through a diseased leaf of wheat in summer reveal the branched and septate hyphae closely packed in the inter-cellular spaces, and investing the green cells. They accumulate below the epidermis, forming a spore-bed, their endings swelling into the *uredo-*

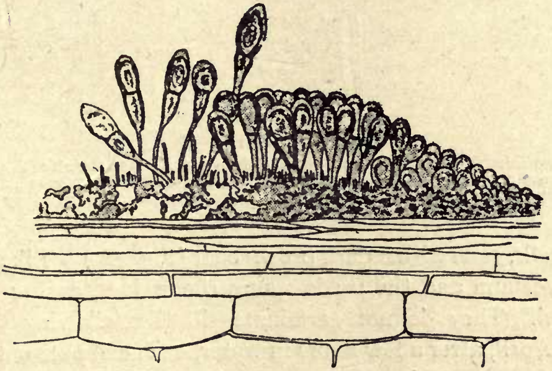


Fig. 380.
Longitudinal section through a patch of the Teleuto-spores of *Puccinia*, on a stalk of Wheat-straw. Highly magnified. (After Marshall Ward.)

spores, which, increasing in bulk and number, burst the epidermis, and are shed (Fig. 377). Each spore is covered by a thick wall, containing dense protoplasm with oily globules, and *two nuclei*. Their walls are marked by thin spots round the equator. It is from these that the germ-tubes emerge when grown in water (Fig. 378). If this germination takes place on a wet leaf of wheat, the tube growing over the surface finds entry by a stoma (Fig. 379), and at once gains access to the nutritive cells. In about a fortnight the infected spot will be producing fresh uredo-spores.

The Teleuto-spores arise from the same spore-bed later in the season. They differ in being closely packed and firmly attached, as well as in structure. Each spore is spindle-shaped, and is partitioned

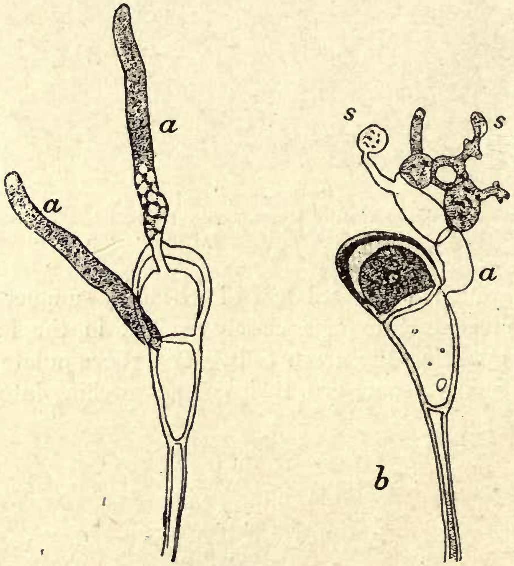


FIG. 381.
Two Teleuto-spores of *Puccinia* germinating. In the one to the left each cell has given off a promycelium (*a, a*); to the right only the lower cell has done so, and the promycelium has given rise to four sterigmata, bearing sporidia (*s, s*). Very highly magnified. (After Marshall Ward.)

into two cells, each with a dark brown coat (Fig. 380). Like other cells of the mycelium and the uredo-spores themselves, each cell contains two nuclei. They do not germinate till the following spring. In March or April, after a few hours in water, each cell puts out a delicate tube (Fig. 381). This, after segmenting to form four distal cells, constitutes what has been called the promycelium, which is a *septate basidium*. The first step is the fusion of the two nuclei: then follows a division into two and into four—in fact a *tetrad-division*, followed by partitioning of the four cells. Each cell then forms a process, or sterigma, on the end of which a swelling appears, and into it the protoplasm and nucleus pass. These are sometimes called sporidia;

but, being the product of a reduction-process, they might properly be called *carpo-spores* (Fig. 381, *s*, *s*). Their peculiarity is that they do not cause infection on the Wheat, but can penetrate the epidermis of the Barberry. Acting on the suspicions already aroused, the

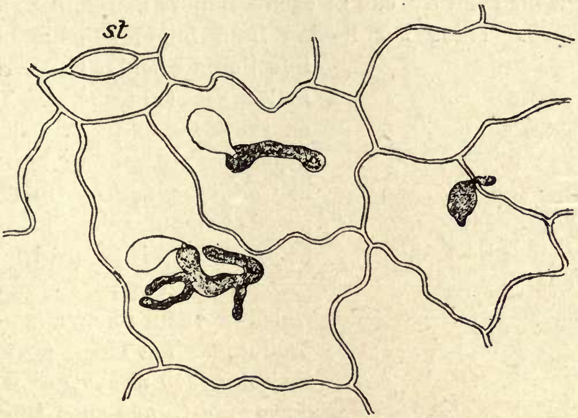


FIG. 382.

Sporidia, or carpospores, of *Puccinia*, germinating on the epidermis of a Barberry leaf, and putting out germ-tubes, which bore through the cell-walls. Very highly magnified. (After Marshall Ward.)

infection was first made by De Bary in 1864. He found that the carpospores easily shed from the sterigmata germinate to form a germ-tube, which can directly penetrate the epidermal wall of the Barberry (Fig. 382). This initiates the second phase, and as the

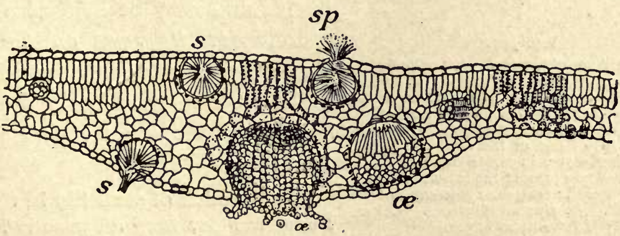


FIG. 383.

Vertical section through a patch of aecidia (*æ*) and spermogonia (*s*) on the Barberry leaf, showing the swelling of the diseased part. The small aecidium to the right (*æ*) has not yet burst. Highly magnified. (After Marshall Ward.)

carpospore itself was haploid, so is the stage produced from it on the Barberry. *Each cell has only a single nucleus.*

A section through an infected spot on the Barberry leaf shows the effect of the attack in the greatly increased thickness as compared with the normal leaf (Fig. 383). The enlarged cells of the mesophyll appear enveloped by fungal hyphae which choke the intercellular spaces. They are massed chiefly at points towards the upper and lower surfaces, to form bodies of considerable size. The first are the flask-shaped *spermogonia* composed of hyphae pointing radially inwards, while from the end of each a minute non-motile *spermatium* is abstricted. These not having been found capable of causing infection, are held to be non-functional male organs (Fig. 383, *s*). The bodies on the lower surface are larger, and develop when mature into the cup-like *aecidium-fruits*. Each is composed of an outer sheath, or peridium, while the cup is filled with filaments rising from the base, from each of which a chain of *aecidium-spores* is produced. The oldest are distal, and they are shed in succession from the downward-turned cups (Fig. 383, *æ*). The ripe spores are *bi-nucleate*. De Bary in 1865 showed that if sown on young grass-leaves they infect them, and produce the Rust again. Thus there are two stages in the life-cycle, which differ in host and in propagative organs: the one has paired nuclei, and may be held as a *diploid sporophyte: it grows on the Grass.* The other has a single nucleus in each cell, and may be held to be a *haploid gametophyte: it grows on the Barberry.*

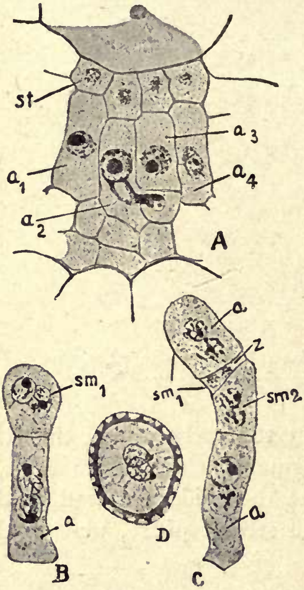


FIG. 384.
Phragmidium violaceum. *A*, portion of a young aecidium; *st*, sterile cell; *a*, fertile cells: at a_2 the passage of a nucleus from a neighbouring cell is seen. *B*, formation of the first spore-mother-cell, *sm*, from the basal cell (*a*) of one of the rows of spores. *C*, a further stage, in which from sm_1 the first aecidiosopre (*a*) and the intercalary cell (*z*) have arisen; sm_2 the second spore-mother-cell. *D*, ripe aecidiospore. (After Blackman.) (From Strasburger.)

The question of sexuality in the Rust-Fungi was for long an unsolved puzzle. There was reason to believe that the spermogonia were rightly recognised as male organs producing non-motile spermatia. The key lay in the early stages of the aecidium. But no carpogonium was to be found there. It is now known that an *apogamous nuclear pairing* occurs, which replaces a sexual process, and initiates the diploid stage with paired nuclei. It has been traced in *Phragmidium violaceum*, as consisting in the passage of the nucleus of one cell into a neighbouring cell, very much as has been seen in certain apogamous Ferns (Fig. 384). But here the nuclei do not fuse at once: the receptive cell remains bi-nucleate, and divides as such into a chain of bi-nucleate spores (*a*), and sterile intercalary cells (*z*) (Fig. 384). Each chain of spores appears to be initiated in this way. A similar process has been seen in *P. speciosum*, and other Uredineae. This discovery made it possible to relate the life-history of the Uredineae to that of other plants. The stage with paired nuclei is held as the correlative of the diploid sporophyte, and that with a single nucleus in each cell as the haploid gametophyte. The events may then be summarised as follows:

A. *Sporophyte on Grass* (paired nuclei).

i. *Mycelium.*
ii. *Uredo-spore* (repeating the mycelium).
iii. *Teleuto-spore* (winter's rest).
iv. *Nuclear fusion* in germinating Teleuto-spore.
v. *Basidium* (=promycelium), equivalent of a spore-tetrad, with *reduction.*
vi. *Carpospore* (=sporidium).
vii. *Infection* of Barberry plant.

B. *Gametophyte on Barberry* (uni-nucleate).

viii. *Mycelium.*
ix. *Spermogonium* (non-functional).
x. *Apogamous nuclear association.*
xi. *Aecidium-spore* (bi-nucleate).
xii. *Infection of Grass-leaf.*

There are many of the Uredineae that do not show so elaborate a series of stages in the life-cycle as the Rust of Wheat. The uredospores may be omitted, or the aecidia; or some may have neither aecidia nor uredo-spores. The spermogonia may also be omitted: so that in these last the life consists of a repetition of teleuto-spores with subsequent germination.

The Rust disease is difficult to check, and its distribution is world-wide. One obvious measure would appear to be to remove the alternative host, the wild Barberry. This has been done in wheat-growing districts in England, but definite consequences from it are uncertain. It is significant that Wheat-Rusts abound in South Africa, Australia, and parts of India, where no species of *Berberis* are indigenous. The most effective remedy is to plant only the seeds of varieties of wheat that are known to be *immune* to the disease, by resisting the infection. Progress has already been made in the production and circulation of such immune varieties. But owing to the minute specialisation characteristic of many Rusts a variety may be immune in one country and susceptible to the same Rust in a different climate: so delicate is the balance which exists between the attacking and resistant powers of two organisms. (Compare Chapter XI, on Irregular Nutrition.)

Ustilagineae (Smuts).

The Smut-Fungi (Ustilagineae) are also parasites on Grasses, certain of them causing diseases on Oats, Barley, Wheat, and Maize, which culminate in the fruiting Ear. The diseased grain is replaced by a mass of dusky spores, corresponding in their behaviour to the teleuto-spores of the Uredineae (Fig. 385). For like them they germinate after the winter's rest, forming a *basidium* (promycelium) with infective *carpospores* (sporidia). These have been shown to be able to infect the seedlings of the corn-plants. The spores may

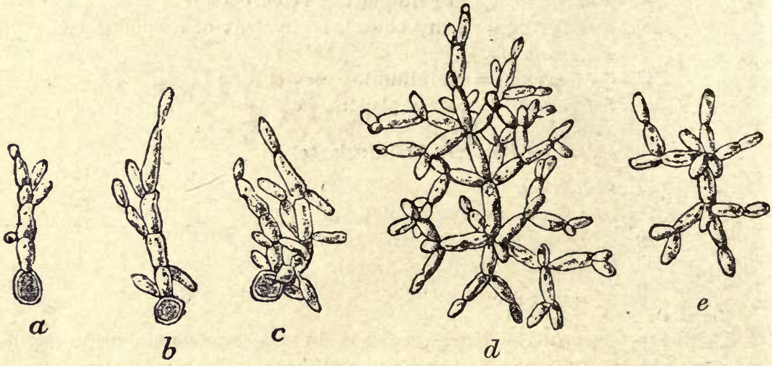


Fig. 385.

Spores of *Ustilago* germinating, and giving off sporidia. (*a*) germinated in water only. *b, c, d, e* in nutritive solutions, where they continue to sprout. Very highly magnified. (After Brefeld, from Marshall Ward.)

have remained on the soil in the field from the previous season; or the crop may have been harvested, and the straw used for bedding, passed to the manure-heap, and then carted out on to the land again. Either way the soil in which the grain germinates will have been infected. A further point of importance is that in a nutritive fluid, like the foul water of the manure-heap, the carpospores formed on germination continue to multiply by *sprouting like yeast*, thus increasing the chances of infection (Fig. 385, *d, e*). It is only the seedling corn that can be infected. The plant once infected grows on as though quite healthy till the flowering period. Then the parasite, the mycelium of which has followed its growth internally, fastens on the ovary, where nutritive material is concentrated, and diverts the food from the formation of the grain to the nutrition of a mass of its own spores. For prevention of the disease "dressing" of the seed-grain with disinfecting mixtures is practised. But equally important is the prevention of the manure being contaminated by the carpospores from the smutted crop of a previous year.

HYMENOMYCETES.

The Life-History of the Rust of Wheat has been described in some detail as giving an example of a Basidiomycete which still shows evidence of sexuality, both morphologically and physiologically:

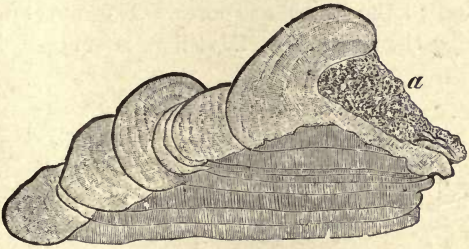


FIG. 386.

Polyporus igniarius. Section through an old fructification, showing annual zones of growth. *a* = point of attachment upon the tree which is its host. The porous hymenium is directed downwards. (½ nat. size.) (From Strasburger.)

though it is altered from what was probably its normal and original course. In the rest of the Basidiomycetes such evidence is wanting. They may provisionally be held to be saprophytes and parasites which were descended from an ancestry with normal sexuality, but have advanced further in the elimination of their sexual process. The Basidiomycetes are characterised by their basidia (Fig. 374, p. 441) borne on fruit-bodies which are often large, of various form and brightly coloured. These are produced upon a *mycelium*, which acquires the necessary nourishment sometimes parasitically, but more commonly from saprophytic sources. The basidia are borne in various ways, and this gives distinctive characters to the main groups of these Fungi. Thus in the *Gasteromycetes* the fructification is closed, the basidia being produced internally, and the spores set free by rupture, as in the Puff-Balls. In the *Hymenomycetes* the basidia are borne collectively in a definite layer

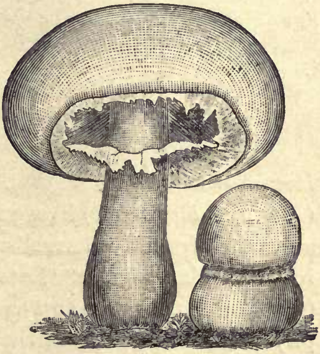


FIG. 387.

Psalliota (*Agaricus*) *campestris*. Mushroom. The hymenium covers the surface of the radiating, downward-directed gills. To the right a young fructification. (Reduced.) (From Strasburger.)

called a *hymenium*, exposed to the air, from which the spores are shed, as in the Mushrooms, Toadstools, and Shelf-Fungi (Figs. 386, 387).

The *mycelium* may obtain nourishment in various ways. It is sometimes parasitic as in the Honey Agaric (*Armillaria mellea*), which penetrates the trunks of forest trees, ravaging the cambium, and killing them (see Fig. 340). Many of the Shelf-Fungi (*Polyporus*) grow parasitically at the expense of the heart-wood of trees, making them hollow. The infection comes through injury by wind, which exposes the internal tissues to the invading spores. The mycelium may live for years, digesting the lignified walls, till it is sufficiently nourished to

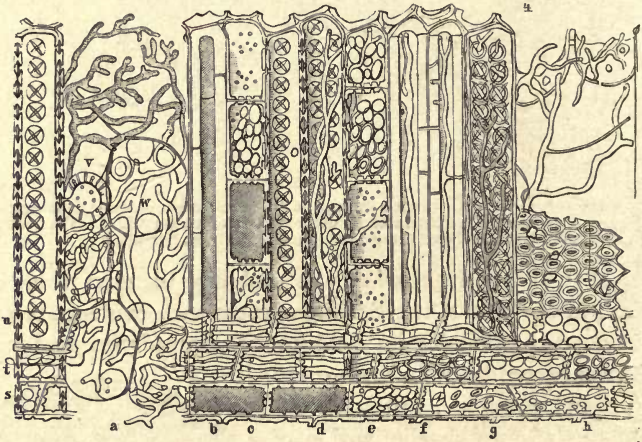


FIG. 388.
Radial longitudinal section through wood infested with *Polyporus igniarius*. Highly magnified. (After Hartig.)

form a fruit-body (Fig. 388). On the other hand the Dry Rot Fungus (*Merulius lacrymans*) lives saprophytically, its mycelium digesting the substance from dead wood-work in houses and ships, where confined in a close damp space. Later it forms the cake-like fruit bodies. The Common Mushroom is an example of a very common habitat of saprophytic mycelium, viz. in the sod of grass-land. It is found especially where horses have been grazing. But the mycelium can be bought in bricks of "mushroom-spawn," made up of a compost of dung, clay, and loam, in which it can be seen as fine white threads, either spreading as single hyphae, or as numerous hyphae running parallel to form thicker strands. If the brick be broken into pieces and spread through a similar compost, and kept warm and moist in the dark, the mycelium spreads; in a few weeks it forms mushrooms of various size. The last stages of development of mushrooms appears to be rapid. This is due to the fact that the tightly packed threads that compose a "button" mushroom (Fig. 387) undergo rapid extension, with absorption of water. The apparently fresh formation of mushrooms from day to day in the fields is thus accounted for. The button-mushrooms are hidden in the grass till the extension takes place.

The Mushroom as commonly known is the fruiting body, borne on the nutritive mycelium. It has the usual toad-stool form, with stalk or *stipe* bearing the hemispherical *pileus* (Fig. 387). As in all large fungal bodies, it consists of false tissue. The hyphae composing it take first a parallel course so as to form the stipe, they then diverge upwards so as to form the wide-spread pileus. In the button stage the margin of the pileus is connected with the stipe by a thin covering of the *velum* ; but this is ruptured as the mushroom expands, leaving a ring round the stipe. The radiating *gills*, which hang vertically from the lower surface, are thus freely exposed. It is upon the gills that the *hymenial layer*, bearing the *basidia*, is borne. The colour of the gills is at first pink, but it gradually grows dark brown with age. This is due to the colour of the spores (*carpospores*) produced in large numbers all over its surface. If a young expanded pileus be laid face downwards upon a sheet of paper, after a few hours a print of the gills will have been traced by deposit of their spores.

A vertical section through the *gills* shows that they consist of a rather lax central region, which supports the more compact *hymenium*, that completely covers their surface. It is composed of narrow *paraphyses* which surround the more bulky *basidia*, the ends of which project, and in the Mushroom bear each two sterigmata, with a carpospore on the end of each. The number two is, however, exceptional among Basidiomycetes. The basidia of the Honey-Agaric are typical (see Fig. 374, p. 441). There the fusion-nucleus divides into four, sterigmata are formed, and one of the nuclei squeezes through the narrow channel into the carpospore which each sterigma bears.

In the Mushroom the germination of the spores presents a difficult problem. It seems probable that one incident, and perhaps a necessary one, is that they should pass through the alimentary tract of some herbivorous animal: for the spores would naturally be taken in with the grass they eat, while the Mushroom grows on old pastures manured by their dung. Related Fungi do not always present such difficulties, and are readily raised from spores. In the case of the Mushroom no other propagative bodies are known, nor has any sexual process been recognised. The fact that in the Hymenomycetes generally a fusion of paired nuclei precedes the tetrad-division, and leads to the formation of the spores, indicates that these are of the nature of *carpospores*. Probably at some stage in the origination of the fruiting body a process leading to a pairing of nuclei will be found. But hitherto it has escaped notice. It seems probable that the fruiting body itself corresponds in the life-cycle to the mass of teleutospores seen in some of the Uredineae. The fact that these may germinate and produce their carpospores *in situ* gives probability to this comparison.

Basidio-Lichens.

Certain Basidiomycetous Fungi take part in the composition of Lichens, but this is much less frequent than in the Ascomycetes. The most familiar example is the genus *Cora*, found not uncommonly in the tropics, growing on the ground or on trees. Its form is not unlike a *Stereum*, or *Thelephora*; and, like them, its hymenium is on the lower surface. The fact that the fungal constituent of some Lichens can be referred to Basidiomycetous Fungi may be held as a final proof of their being coalition-organisms (see pp. 438-440).

Fungi as Subaerial Plants.

The Fungi, sprung probably from various Algal sources, show some degree of adjustment to subaerial life parallel to that already seen in Green Plants. But as the hypha is the basis of their construction, their vegetative system gives less opportunity for adaptive change than their propagative organs.

The most striking modifications are seen in the Phycomycetes, which are referred in origin to non-septate Algae having motile zoospores and gametes. Among the Oosporeae the aquatic origin is clearly reflected in the germination of the conidia, where each bursts and gives rise to zoospores motile in water (Figs. 351, 355, pp. 415, 420). The conidium here appears in fact to be a sporangium like that seen in many Algae, but reduced in size and detachable, so as to secure the spread of the organism through air, though its germination is still carried out in water. Similarly in the Zygosporeae the large sporangium of *Mucor* is also effective for water-distribution of its spores, though they are not themselves motile (Fig. 360, p. 425). But within the family of the Mucorini the sporangium is liable to be reduced in size, with increase in its numbers, till in *Chaetocladium* and *Pipto-*

cephalis it matures as a single detachable cell. In fact it is an air-borne conidium, their large numbers being a set off against the unicellular condition of each. The Oosporeae and Zygosporeae thus suggest a parallel progression from sporangia producing numerous germs to small wind-borne bodies, ranking as conidia. The profuse propagation of the Eu-mycetes by various types of detachable unicellular spores, also called conidia, acts biologically in the same way, as a means of sub-aerial propagation and distribution. But the phyletic origin of such spores was probably from a source distinct from that of the Phycomycetes.

On the other hand, the sexual organs in *Pythium* and *Cystopus* correspond in form and general characters to those of the Siphoneae, such as *Vaucheria*. But in place of a dehiscent antheridium, shedding spermatozoids motile in water, a fertilising tube is found, which, like a pollen-tube, transfers its contents directly to the ovum (Fig. 357, p. 422). It is in fact an antheridium, which being sub-aerial in its development does not dehisce to set free motile gametes. In the Mucorini the zygospores may very probably be regarded in the same way, but referable to a more primitive state of sexuality. Two distal gametangia, instead of dehiscing and their separate gametes fusing, conjugate as a whole, producing the coenocytic zygospore (Fig. 345, p. 410). This may be held as a sub-aerial modification of the conjugation of gametes of the type seen in *Bryopsis*. Such examples do not provide so coherent a series as the green Plants do. But they accord with the general reference of Land-living Plants in their origin to an aquatic ancestry; and they illustrate how the modifications in Thallophytes may run parallel with those of organisms higher in the scale. Such parallels go far to support the general thesis that Plant-Life originated in the water, and spread later to land-surfaces.

CHAPTER XXX.

SCHIZOPHYTA.

UNDER the general name of the Schizophyta a vast number of minute organisms have been included, which have multiplication by fission as a common feature. The closeness of their affinity is, however, a question of some doubt. Some of them possess colouring matter of a bluish-green or pink tint, and are therefore distinguished as Fission-Algae, or *Cyanophyceae*. In others such colouring is wanting in the protoplast: they are distinguished as Fission-Fungi, or *Bacteria*. These are among the simplest of organised plants, and include the most minute of living beings. They stand rather isolated from the other Thallophytes. Most of them have more or less gelatinous walls, surrounding a protoplast in which, though granules of chromatin may be detected, there is no fully organised nucleus. Sexuality is absent. But in contrast to this simplicity of structure and life-history they show the greatest possible variety of physiological activity, and this is especially so among the *Bacteria*.

CYANOPHYCEAE.

The blue-green Algae are unicellular, or filamentous. They are found living either in water, or on surfaces which are habitually moist. A common type is seen in *Gloeocapsa*, where the oval or spherical cells have a swollen cell-wall. This holds the cells together after fission, in rounded colonies which break up by disorganisation of the wall. It is commonly found on the inner surfaces of the glass of damp greenhouses (Fig. 389).

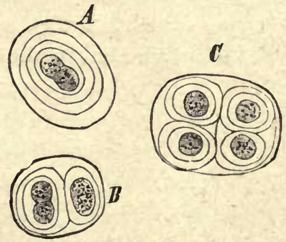


FIG. 389.
Gloeocapsa polydermatica. *A*, in process of division; *B*, to the left, shortly after division; *C*, a later stage. (× 540.) S.

Oscillatoria is a filamentous type, which is common on damp walls and rocks. Its pale green filaments show slow swinging movements, hence the name (Fig. 390). They consist of disc-shaped cells, which multiply by division. In some of the larger forms granules of irregular form are found in each cell, giving the staining reactions of chromatin, and dividing before division of the cell, but without a definite nuclear spindle. The filaments may break up at any point into shorter lengths, and are unattached. In other cases special cells (heterocysts) occur at intervals in the filaments, which appear to determine their breaking up into shorter lengths, as in

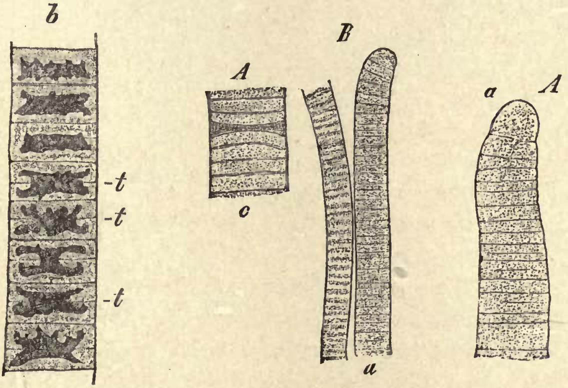


FIG. 390.

A, *Oscillatoria princeps*: a terminal portion of a filament; *b*, portions from the middle of a filament, properly fixed and stained; *t*, cells in division. (× 1080). *B*, *Oscillatoria Froelichii*. (× 540). S.

Nostoc or *Rivularia*. Some of these fission-Algae take part in the formation of Lichens: thus *Collema* has *Nostoc* as its Algal constituent. Others, such as *Anabaena*, lead an endophytic life, contributing probably to an irregular nutrition, as in the roots of Cycads. In the establishment of the new Flora of the sterilised Island of Krakatoa (p. 295), blue-green Algae were among the first colonists, taking their part in the preparation of an organic soil for larger developments to follow. Certain of these Algae allied to *Anabaena* often appear suddenly in large quantities on the surface of fresh water, causing the phenomenon known as "water bloom," or the "breaking of the meres." One of these, with a deep red colour (*Trichodesmium erythraeum*), floats in ocean-waters, and becomes prominent when massed together by wind and tidal streams. It has thus attracted attention in various oceans, and has given its name to the "Red Sea."

BACTERIA.

The relation of the *Bacteria* to the Cyanophyceae is obscure. But they certainly offer many points of analogy in their mode of life. They are unicellular or filamentous organisms, without chlorophyll, and they lead a parasitic or saprophytic existence. Their cells may be spherical (*Coccus*), or rod-shaped (*Bacillus*), or slightly spiral (*Vibrio*), or strongly spiral (*Spirillum*), or straight and slender (*Cladothrix*), or grouped in cubical packets (*Sarcina*). They have a superficial membrane, and protoplasmic body, sometimes with chromatin-granules, but no definitely formed nucleus. Many of them are motile, and bear cilia varying in number and position in different types. Their multiplication is by fission. Their mode of life is best illustrated by an example.

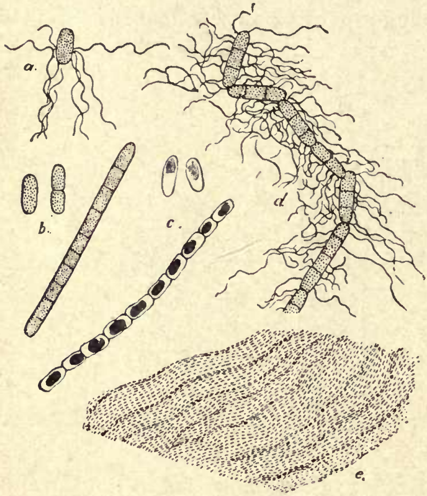


FIG. 391.

Bacillus subtilis. *a, d*, motile cells and chains of cells; *b*, non-motile cells and chains of cells; *c*, spores from the zoogloeae; *e*, the zoogloea. (From A. Fischer. *a-d* × 1500; *e* × 500.) S.

The Hay-Bacillus (*B. subtilis*) can be obtained in any decoction of hay, in hot or even in boiling water. If the fluid is filtered and set aside for 48 hours it will be found to be swarming with ciliated Bacilli, while at the surface a scum is formed, which is the "zoogloea" condition of the same plant. In old hay the *Bacillus* is in the resting condition, as spores, the protoplasm having contracted away from the wall, and being surrounded by a thick membrane (Fig. 391, *c*). The spores can resist even the temperature of boiling water, and pass still living into the decoction. There they germinate into active Bacilli, motile in the fluid by cilia (Fig. 391, *a*, *d*). But those which rise to the surface lose their motility (*b*), though continuing to divide; they form thick gelatinous walls, and so they remain associated together as the scum of the zoogloea (*e*). If the supply of organic material is exhausted they pass again into the resistant spore-stage. It thus appears that a single boiling of the medium containing spores of *B. subtilis* is not enough to sterilise it, for the spores can resist

100° C., at least for a time. For complete sterilisation it is necessary after boiling to incubate the culture at a favourable temperature of 37° C. for 48 hours, during which time the spores will all pass into the active but vulnerable state. Then a second boiling will completely sterilise the fluid. This method is commonly used in the preparation of media for the culture of Bacteria.

It is important to realise the great rapidity of multiplication of Bacteria. Under favourable conditions *B. subtilis* is found to divide once in about 20 minutes. If this pace be continued by all the progeny for 8 hours the result from a single Bacillus would be over 16 millions. It is not, however, the rapid multiplication and easy transfer of these minute bodies alone which gives the Bacteria their importance. A still more interesting feature is the variety of their physiological powers. Being as a rule parasitic and saprophytic plants, they depend for their supply of food and energy upon breaking down more complex into simpler compounds: and they do this in the most various ways. The end of all such changes is ultimately carbon-dioxide and water. In fact, Bacteria are the great scavengers of the world, restoring organic material to the sources from which it came. But in the course of the process many steps may intervene: and bye-products may be produced which are sometimes useful, though often harmful to other organisms, and to Man. Thus the Bacteria that cause various diseases release into the blood or tissues, toxins or poisons which give the several diseases their character. On the other hand changes wrought by Bacteria may be beneficial in various ways: for instance, the nitrifying Bacteria convert ammonia into nitrous, and finally into nitric acid, present in the soil as nitrates; acetic-acid-bacteria may convert alcohol into vinegar; and *Rhizobium* may fix free nitrogen in the root-tubercles in which it grows (p. 204). Again, the flavours of cheese, butter, or tobacco, and of many other commodities, depend for their market-value upon the exact type and conduct of the partial decomposition of their constituents by bacterial action.

Where suitable material is available Bacteria may multiply indefinitely. But there are important external checks which control them. Many Bacteria are susceptible to injury by light. This has been shown for the Anthrax-Bacillus, by growing it on culture-plates, partly exposed to light and partly shaded; and the results have been verified in various others. The destructive effect lies in the blue-violet end of the spectrum. After incubation in the dark for three or four days, the area of a plate exposed for a time to such rays at the beginning of the experiment will remain clear, while the shaded portion will be covered by bacterial colonies: showing that the bacteria exposed to light had been killed. Such facts are of prime importance in relation to general health: for sunlight thus offers a natural and wide-reaching check upon the spread of many harmful germs.

The relation of Bacteria to the free oxygen of the air is also a matter of importance. Like other organisms they may be distinguished as aerobic and anaerobic, according to their dependence upon the presence of free oxygen, or their independence of it (p. 115). But no sharp line can be drawn between these two modes of life. Many Bacteria carry on their life with absorption of oxygen, like other plants. But some of the most deleterious, such as the Bacillus of Tetanus, flourish only in the absence of free oxygen, obtaining their supply of energy at the expense of the organic material which they destroy. Such activity may be compared with that of the bottom-yeast of beer-vats, both being anaerobic. It is this mode of life, together with the toxins which result from it, that makes the Tetanus-Bacillus specially dangerous in wounds.

Such questions as these are, however, the material for more special treatises than this. It must suffice here to have pointed out that the partial decompositions due to bacterial action are of most varied importance, economically and socially. Physiologically they may be referred for the most part to that degradation of organic material which supports parasitic and saprophytic Life.

On the basis of nutrition Bacteria have been classified into three groups: (i) *Prototrophic*, those which require no organic compounds at all for their nutrition. These are represented by the nitrifying Bacteria which live in open nature, in the soil, and are never parasitic. (ii) *Metatrophic*, those which cannot live unless they have organic substances at their disposal, both nitrogenous and carbonaceous. They occur in the open, and are saprogenic and sometimes parasitic (facultative parasites). (iii) *Paratrophic*, those which develop normally only within the living tissues of other organisms, and are true, and obligatory parasites, such as the germs of Tubercle or Diphtheria.

This classification may be extended, however, to all other organisms. All green autophytes are prototrophic in the same sense as the first group of Bacteria. All fungi and animals are metatrophic, except the parasitic forms, which are paratrophic. Thus the Bacteria exemplify types of nutrition which run parallel with those seen in larger organisms.

CHAPTER XXXI.

SEX AND HEREDITY.

In the great majority of Plant Organisms certain sexual cells called *gametes* are produced, which fuse in pairs. The process is called *Syngamy*, or *Sexual Fusion*. The result of it is the production of a single cell, the *Zygote*, which forms the starting point for a new individual. Though such syngamy is a very wide-spread fact among living things, whether Animals or Plants, it is not universal. Some primitive organisms are without it. The whole series of the Schizophyta are examples of this, while further instances are seen in *Euglena* and *Protococcus*. In certain Plants also of advanced organisation syngamy may be absent, as in some Flowering Plants and Ferns; and notably in the higher Basidiomycetous and Ascomycetous Fungi. There is reason to believe that in such cases syngamy has been omitted or lost, for comparison indicates that all these plants have been descended from a sexually propagated ancestry. Thus syngamy, though prevalent, is not an indispensable feature in every life-cycle.

A comparison of related organisms low in the scale, which show syngamy, suggests that in the first instance the fusing gametes were alike in size and behaviour, though more or less distinct in their origin. Such cells are called *isogametes*, and the process of their fusion is described as *conjugation*. It is seen in both Animals and Plants of low organisation. This condition, where the gametes show no clear distinction of sex, is believed to represent a primitive state from which distinction of sex was later derived. The isogametes themselves may be motile or non-motile. The former is seen typically in various green and brown Algae: *Ulothrix* (Fig. 330, p. 392), *Acetabularia* (Fig. 335, p. 397), and *Ectocarpus siliculosus* (Fig. 321, p. 383) are cases in point. Conjugation of non-motile isogametes occurs in the Conjugatae, such as *Spirogyra* (Fig. 337, p. 399).

If two organisms, each consisting of only a single cell, fuse to form one, the immediate result is a diminution in number to one half. This occurs in various instances, and *Spirogyra* is a case in point, for each cell of its filament is properly recognised as an individual. The same occurs in various other unicellular Animals and Plants. As these are probably primitive, they suggest that in the first instance syngamy was not a means of increase in number of individuals, though in all the higher Plants and Animals this appears to be its natural consequence. Some believe that the chief advantage following on sexual fusion in such simple organisms lay in nutrition. If during repeated fissions cell-division was more rapid than nutritive recuperation, then fusion of two cells would be a possible form of recovery. But such fusion appears to bring with it also a stimulus to fresh activity of growth and division, which may break out at once, though in primitive organisms it follows usually after a period of rest. With this fusion there follows also the pooling of such qualities as the fusing cells themselves possess. So far as these qualities can be transmitted to the offspring, the mechanism of fusion offers the opportunity for their transmission; and it is significant that the fusing gametes are as a rule distinct in origin. For instance, the pairing gametes of *Ulothrix* (p. 392), or of *Ectocarpus* (p. 383), originate from different gametangia; and the distinctness of origin is still more marked in many plants higher in the scale. It seems probable that such advantages as these, viz. nutritive recovery, stimulus to further development, and hereditary transmission, have favoured a constant recurrence of syngamy. In the long run hereditary transmission has been the most important.

Differentiation of Sex.

Fusion of isogametes once established led to sexual differentiation in many distinct phyletic lines, both of Animals and Plants. Comparison of closely related forms is the basis of this conclusion; and a particularly convincing example is seen in the Brown Algae (pp. 380-385). The distinction is there found to be first a difference in behaviour rather than of form (*Ectocarpus siliculosus*). Next, a difference in size as well as in behaviour marks the female as distinct from the male, as in *E. secundus*. In *Cutleria* that difference is still more accentuated, and the larger female gamete soon loses its motility. In *Fucus* the difference in size is very great indeed, and the large female egg is never motile at all. Various other phyletic lines could be quoted showing similar examples of differentiation of sex (Fig. 335). The question naturally arises why should such progressions exist in a plurality of distinct phyletic lines? That the differentiation of sex has occurred more than once indicates a probability that some real advantage has prompted it.

The advantage appears to lie in the fact that the larger the amount of nutriment embodied in the egg, the better nourished the offspring will be in its first stages, and the better accordingly will be the chance of its passing successfully through the dangerous risks of youth. But the larger the egg the less mobile it will be. Even in the liquid medium into which the eggs of Algae are often shed, a large body is less easily moved than a small one. We naturally associate with this the fact that the larger eggs have lost their motility. This is, however, immaterial so long as the spermatozoids remain small and actively motile, provided that the egg can influence their movements, and so act as a centre of attraction to them. It has been seen that the eggs are able to do this (p. 386). Such advantages as follow from the stimulus of fusion, and the pooling of the hereditary factors of the two sexual cells can still be secured by these means. Thus the nett advantage lies with the plant which can, without sacrificing the benefits that follow from syngamy, secure also for its offspring an increased probability of successful germination. Conjugating organisms, with their small equivalent gametes, may be regarded as a plant-proletariat that produces numerous offspring with little physiological capital; so that each individual must depend chiefly upon its own efforts. The organism that shows differentiation of its gametes with an enlarged well-nourished egg is like a capitalist, whose progeny starts life well furnished with an inheritance. Other things being equal, ultimate success will lie with the latter. Both Kingdoms of Living Beings show how successful the results of sex-differentiation have actually been: for all their higher terms have differentiated gametes.

A large naked egg, such as that of *Fucus*, may be a successful enough means of propagation in water. But it could not develop into an embryo exposed to the drying influence of the atmosphere. A necessary condition of Life on the Land is thus the protection in one way or another of the egg and the embryo. In the Evolution of Land-living Plants and Animals this necessity has played a leading part. The result is seen in the various forms of *internal embryology*: that is, the envelopment of the egg and of the embryo within the tissues of the parent. This brings also the collateral advantage of its continued nutrition. How this has worked out in detail in Mosses and Ferns, and ultimately in the Seed-Plants, will be discussed in Chapter XXXII. Here it must suffice to remark that the subsequent changes seen in such Plants have to do with the details of transmission and of nursing of the gametes. They do not involve any further distinction of the male and female gametes, in respect of size or structure, than that already established among the Higher Thallophyta.

Functions of Sex.

To form an opinion on the function of the gametes in sexual propagation, a knowledge of their structure is necessary; also of the relation of their structure to that of other cells of the plant-body. The nucleus, which takes a prominent part in the process of fertilisation, and itself constitutes almost the whole of many spermatozoids, will specially claim attention. Moreover, the facts already recognised in Chapter II., p. 22,—that every nucleus is derived from a pre-existing nucleus, and that in ordinary cell-division the parent nucleus is partitioned into two exactly corresponding halves,—suggest that the nucleus has a special relation to the facts of heredity. The detail of the process of division of the nucleus of an ordinary somatic cell will then be the natural starting point for the further discussion of Sex and Heredity.

Somatic Division.

The resting nucleus of a vegetative cell has a reticulate structure. The network is recognised chiefly by the punctated appearance of the anastomosing threads. These threads consist of a substance called *linin*, which bears minute granules of *chromatin*, so called because they take up certain stains more readily than the rest of the nucleus. One or more *nucleoli*, composed probably of reserve material, are closely connected with the network, while the interstices are filled with *nuclear sap;* and the whole is delimited by a *nuclear membrane* (Fig. 392, i.). When such a nucleus is about to divide, the network is drawn together at a certain number of points, round which bodies, at first irregular but ultimately of filamentous form, are segregated. They take a deep stain, and are accordingly called *chromosomes*. It is probable that they maintain their identity, though in a diffused form, during the resting period of the nucleus, but become evident by their condensation as division approaches (Fig. 392, ii.). They group themselves in an equatorial plane, which corresponds to the plane of division of the cell. Thus placed they constitute what has been called the nuclear, or equatorial plate (Fig. 392, iii.). Each such chromosome splits longitudinally, and the *two equivalent halves* separate and move apart, the one to form a constituent of one daughter nucleus, the other of the other (iii. iv.). The mechanism by which this separation is carried out is by cytoplasmic filaments, which originate outside the nuclear membrane. Their position is at first irregular, but presently they become arranged so as to con-

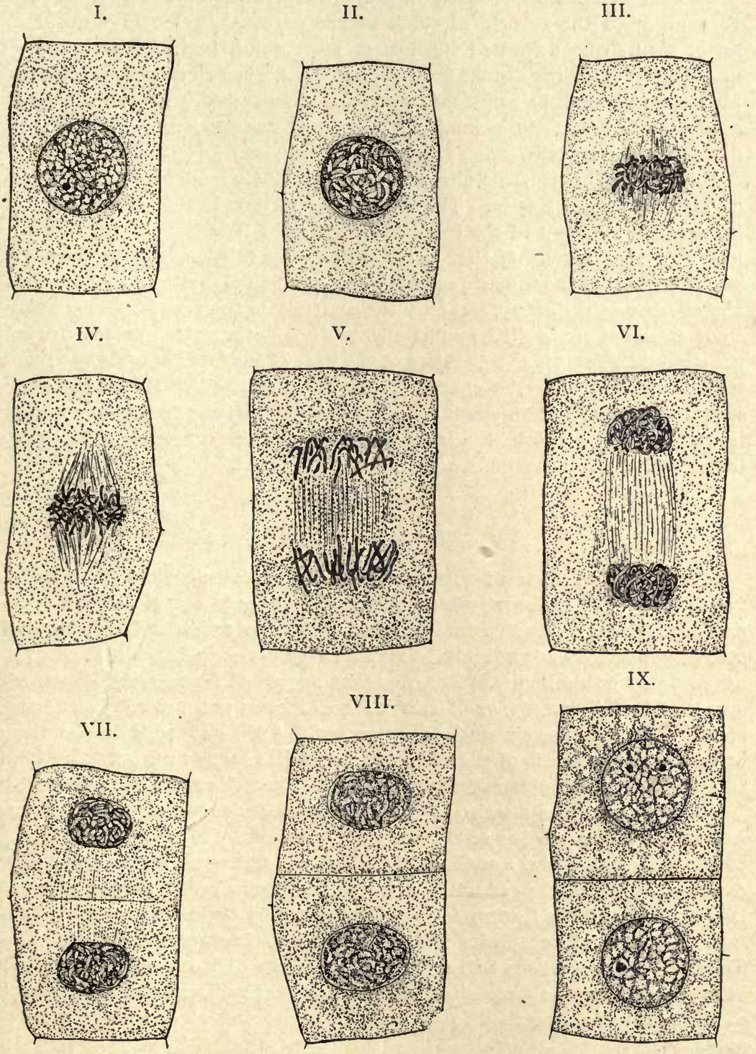


FIG. 392.
Successive stages of division of somatic cells of the same root of *Allium cepa*, drawn by Dr. J. M. Thompson. (× 730.) For detailed description see Text.

verge to two poles, thus constituting the nuclear spindle (iii. iv.). The nuclear membrane cannot now be recognised, and the half-chromosomes attached to the spindle-fibres appear to be drawn apart, and converge towards the poles, thus constituting the basis of two fresh and equivalent nuclei (v.).

The further changes consist in the reconstitution of the two new nuclei, through steps the reverse of those at the outset. Presently the nuclei are again seen to be delimited by nuclear membranes (viii.); the chromosomes gradually recover the diffuse form (vi. vii. viii.), nucleoli reappear, and the two nuclei correspond in appearance to the parent (ix.). Meanwhile granules appear in the equatorial plane (vii.), which coalesce and form the partition-wall dividing the new cells.

By this mechanism the chromatin of the parent nucleus is very exactly divided into equal halves. The view is generally held that special functional importance attaches to the chromatin, and that it is the chief carrier of the heritable characters. If that be so, a mechanism is present in the division of the nucleus of the somatic cell by which the nuclei multiply without materially changing the quality, but only the quantity of their chromatin-substance: since an equal share of the substance of each chromosome passes to each of the new nuclei. It is this that lies at the base of the fact that somatic budding repeats very exactly the characters of the parent plant: for, as has been seen in Chapter XII., the buds all originate vegetatively, that is by multiplication of cells by somatic division; and each constituent nucleus will accordingly bear the full heritable qualities of the parent.

Tetrad Division.

It is, however, different with those rapidly successive divisions,—first into two and then into four,—which occur once in each completed life-cycle of any sexual plant. Such *tetrad-division* habitually precedes the formation of spores, which may accordingly be styled *carpospores*, to distinguish them from other propagative bodies. Pollen-grains, spores of Ferns and Mosses, tetraspores of Red Seaweeds, or of *Dictyota*, ascospores, and probably also basidiospores are examples of such carpospores. All these initiate the haploid or gametophyte phase of the life-story; and this fact draws special attention to the details of the tetrad-division which brings them into existence.

Fig. 393 represents a series of twelve accurate drawings, made under *camera lucida*, of pollen-mother-cells of *Allium ursinum*, the Common Garlic, all to the same scale, viz. × 1000. They illustrate successive stages in the tetrad-division, by which the reduction of chromosomes to half the original number is effected; and the leading features of it are of general application.

1. The general cytoplasm is of a dense and finely granular appearance. The *nuclear membrane* is well defined. There is a delicate network of threads of *linin*, on which the *chromatin* is more or less evenly distributed. The meshes of the network are bathed in clear *nuclear sap*, and at one point there is a *nucleolus*.

2. The spore-mother-cell has enlarged, and at the corners its wall is separating from those of the neighbouring cells. The nuclear sap has greatly increased, but there is no noteworthy increase in the chromatin-bearing linin, which now lies mainly on one side of the nucleus, as a kind of tangle, involved in which are two nucleoli. This stage of nuclear-division in the tetrad is known as *synapsis*.

3. The spore-mother-cell has now completely separated from its neighbours, and is roughly spherical. The nuclear enlargement noted before is

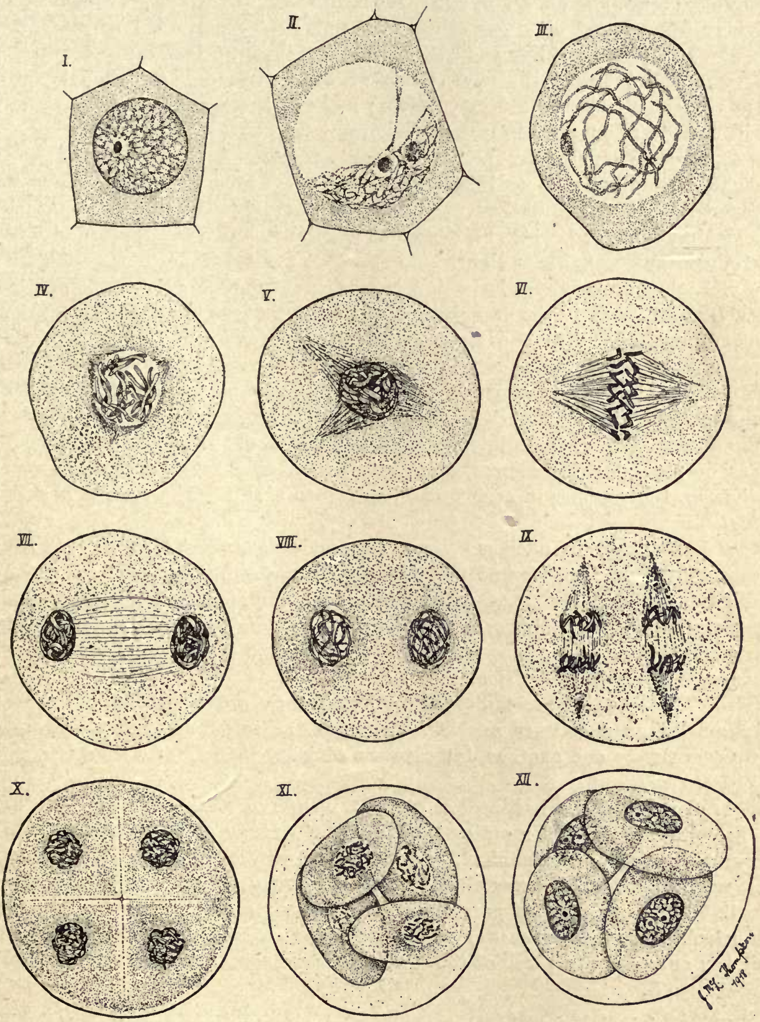


FIG. 393.

Drawings by Dr. J. M. Thompson, representing in detail twelve successive stages in the tetrad-division of the pollen-mother-cell of *Allium Ursinum*. (× 1000.) For the detailed description see Text.

maintained, but the linin-reticulum is resolved into a definite number (in this case sixteen) of slender *chromosomes*. A nucleolus is still recognisable.

4. The volume and amount of nuclear sap are now diminished. Several conical groups of *fibre-like lines*, of which three are seen in the section, pass from the nuclear membrane into the cytoplasm. *The chromosomes are now short and thick, and appear in pairs*, the individuals of each pair being more or less spirally wound upon one other. There is no recognisable nucleolus.

5. The nuclear volume is further decreased, and nuclear sap is no longer recognisable between the now closely grouped chromosomes, around which the nuclear membrane is closely drawn ; meanwhile the fibre-like lines already mentioned are aggregated towards several poles.

6. Two such poles are here prominent, forming a *bipolar spindle*. The nuclear membrane is no longer recognisable. From the tangle of paired chromosomes, which marked the preceding stage, sixteen *short dense chromosomes* have emerged, which are placed equatorially, and are segregated into two groups each consisting of eight.

7. Eight chromosomes have now passed towards each pole of the spindle. Each group leads to the organisation of a fresh nucleus, with distinct nuclear membrane, and with the eight *chromosomes* interwoven, but still clearly recognisable. Between the two nuclei stretches a system of spindle-fibres.

8. The fibres have disappeared. Nuclear sap is present between the chromosomes in both nuclei. Since sixteen chromosomes were involved in the organisation of the original nucleus, and each of the two daughter nuclei has only eight chromosomes, *this first division is a heterotype, or reduction-division*, the number in each being reduced to a half. The process is styled *Meiosis*.

9. Each daughter nucleus s here undergoing a *second division*. In each case the nuclear membrane and the sap have disappeared, and a bi-polar spindle has been organised around the eight chromosomes, arranged again equatorially. *Each chromosome has halved longitudinally*, and a group of eight chromosomes is moving towards each spindle-pole. This second division is a *somatic, or homotype division*.

10. The spindles have disappeared, and each group of chromosomes is organising as a distinct nucleus. Between the nuclei lines of cleavage, at right-angles to one another, indicate the division of the mother-cell into *four daughter-cells*.

11. Each nucleus has now a distinct membrane, and nuclear sap. The chromosomes are still more or less distinct. Around each nucleus a definite cytoplasm has been organised, and is enclosed within its own spore-wall.

12. The *tetrad of spores* thus formed lies freely within the spore-mother-cell. Each nucleus has passed into the reticulate stage, with one or more nucleoli. *As a consequence of the reduction each nucleus is now haploid*, that is, it has only eight in place of the original sixteen chromosomes of the spore-mother-cell.

The critical point in the process of tetrad-division in its bearing on Sex and Heredity is in the stage preceding its first nuclear division (Fig. 393, III.-V.). Many detailed observations have shown that as they emerge from "synapsis" the original chromosomes are paired, lying with their longer axes parallel, or closely coiled together. Subsequently the members of each pair separate, one chromosome of each pair passing to one pole, the other to the other pole of the first spindle (VI.). There is, in fact, a sorting of the members of the several pairs to constitute the new nuclei, the number passing to each being half of the total. Thus, if there were $2x$ chromosomes in the nucleus of the mother-cell, each of the new nuclei would consist of only x chromosomes. If, as there is good reason to believe, the chromosomes in some way represent or convey hereditary qualities, then by this *reduction-division*, or *meiosis* as it has been called, *those qualities will be segregated into two groups, and the daughter-nuclei will not be functionally the equivalents one of another.*

The difference between this and a somatic division may be illustrated by a diagram. If a simple case be taken, with six as the

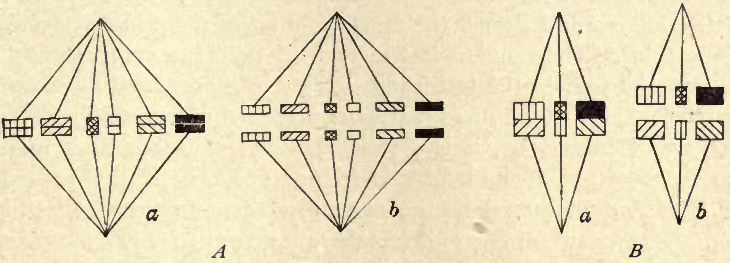


FIG. 394.

A, Diagram illustrating the behaviour of the chromosomes in somatic division, when the number of chromosomes is six. (After Strasburger.)

B, Diagram showing the behaviour of the chromosomes in Meiosis, where the number six is reduced to three by segregation into two groups. (After Strasburger.)

diploid and three as the haploid numbers, and the specific qualities of the individual chromosomes be indicated by differences of shading, then Fig. 394 *A*, *a*, *b* might represent what happens in a somatic division. Each chromosome being halved, and the halves diverging to either pole, each new nucleus there formed will have an equivalent representation of each chromosome, with the qualities which it bears. But in the reduction-division, since the chromosomes pair and separate again, and since three of these converge *as whole chromosomes* to each pole, it is clear that the two new nuclei will not have an equivalent representation of the qualities of all the six chromosomes, but only of three of them (Fig. 394 *B*, *a*, *b*). The meiosis, or reduction-division, has segregated them into two groups. This is the essential point in the first or *heterotype* stage in the tetrad-division. The second stage is a *homotype* division, that is carried out like any somatic division, and the nuclei of each resulting pair will be equivalent one to another. *Thus in each tetrad there will be two cells or spores of the* *one type and two of the other.* Since the spores of these two types germinate, and each gives rise to a gametophyte, and ultimately to the gametes, it follows that *the gametes produced from these two types of spore will not be all alike, but will share the same segregation of characters as the spores that gave rise to them.*

A second point is that the reduction of chromosomes to one half having taken place in the tetrad, all the succeeding products of their germination will be on the reduced or haploid footing, having only x chromosomes. This applies to the whole gametophyte generation, and to the gametes themselves, which are haploid.

Fertilisation consists in the fusion of gametes. In many Algae these are clearly primordial cells, with cytoplasm and nucleus. But as the spermatozoids became more specialised in higher types, such as the Mosses and Ferns, their cytoplasm was reduced to negligible proportions. The opinion is widely held that the cytoplasm takes no essential part in the fertilising process beyond acting as a carrier for the male nucleus, or as a storage place for nutriment in the egg. However this may be, it is certain that the nucleus makes up the great proportion of bulk of the spermatozoid both in the higher Animals and Plants, while the most prominent features in fertilisation arise from the male and female nuclei. The former passes into the cytoplasm of the egg: it approaches, and applies itself to the female nucleus. The nuclear membranes disappear along the surface of contact. Both nuclei have been seen in favourable cases to enter the so-called spireme state with disengaged chromosomes, as if about to divide. The male and female chromosomes pair, and subsequently each divides transversely. One half of each of the pairs moves to either pole of the first nuclear spindle of the zygote, so that the male and female elements are equally distributed. Both male and female gametes being haploid when fertilisation takes place, the double number of chromosomes is restored. The diploid sporophyte is thus initiated, and the chromosome-cycle,—sporophyte,—gametophyte,—sporophyte,—may be repeated indefinitely.

Hybridisation.

If the gametes involved in producing such a succession of generations were uniform throughout in their origin and in all their characters, the organisms produced might be expected to remain constant. But the parents that produce the gametes are not themselves exactly alike, and the gametes produced from them will therefore differ. Differences exist between individuals, strains, varieties, species, and genera, and so on. By gradual steps one may thus pass from the similar to the strongly dissimilar. Within certain limits the dissimilar can breed together: for instance, individual strains and varieties commonly interbreed. Sometimes species and even genera can produce offspring together. The bi-generic crosses of certain Orchids artificially produced are a well-known feature of horticultural shows. In seed-bearing Plants the seeds produced by crosses from distinct parentage may germinate, though where the parents are strongly dissimilar either there is no offspring, or it is apt to be itself sterile, as is the mule. Thus a limit is set upon distinctness of parentage. Such crosses between parents more or less dissimilar are called *hybrids*, and they are characterised by sharing in greater or less degree the qualities of both parents. So far as qualities can be transmitted from parent to offspring, the mechanism of sexual fusion offers the opportunity for their transmission. There is no doubt that Heredity is a fact; but the sexual transmission of characters is governed and limited by certain laws which restrict its scope. The result is that while the sexually produced offspring shares the characters of both parents, it practically in all cases differs in some degree from each of them. It is a matter of common observation that it does not repeat *all* the characters of *both* parents.

The characteristics of organisms have been classed under two heads: those which are heritable and are transmitted, and those which are not. The former includes such features as have not been referred directly for their production to the impress of external circumstances upon the parent. The latter include those features which can be so referred. It may, however, be a question how far these categories are mutually exclusive. As examples of those not transmitted mutilations may be quoted; or the immediate accommodations of the growing parts to the impress of gravity, light, etc., such as are described in Chapter VIII. However effective these may appear to be in determining the mature form of the parent, there is no sufficient evidence that these specific results are handed on to the offspring. They are described as *fluctuating variations*. But there are other larger or smaller deviations from type, appearing suddenly and individually, which have not been referred directly to known causes, and are found to be heritable. These have been called "*Mutations*." The numerous minor deviations from type in *Draba verna*, described by Jordan, are cases in point. The fluctuating variations appear to leave no permanent impress upon the organism, so as to affect its gametes. The heritable mutations, on the other hand, appear to arise from qualities in some way impressed upon the gametes, and so transmitted to the offspring. The line between these two types of variation is often sharply drawn, and it has been stated dogmatically that characters acquired in the lifetime of the parent are never transmitted to the offspring. *Without going so far as that, it is permissible to state that hitherto the evidence of the inheritance of characters acquired during the lifetime of the parent is insufficient.* On the other hand it is believed that mutations which can be transmitted from parent to offspring have played a great part in Evolution. They provide a basis upon which Natural Selection can work.

Various "adaptations" of structure to external conditions have been described in Chapter X. Instances have also been cited of parallel development, or homoplasy, where in series of plants distinct by Descent, similar adaptive modifications are seen (pp. 177, 193, 210, etc.). Such results are usually set down to the selection of favourable divergences from type out of inheritable variations, or mutations, produced at random. But the prevalence of parallel development, and even of convergence of characters, suggests that the mutations upon which they have been built up were not produced at random. That possibly the origin of "mutations" may be directed by some internal or physiological necessity. That they may have been promoted or actually determined in their direction, or their number, or their quality, in some way by the external conditions. In fact that they may have been acquired,—either in the course of the individual life, or cumulatively of a succession of lives,—as consequences of the impress of external conditions. The question of the origin of mutations, great or small, is still a quite open one. It is better to entertain the possibility of some such acquisition of mutations as a working hypothesis than positively to deny it. This is one reason why the doctrine of inheritance of acquired characters has not been ruled out in the preceding paragraphs. Its negation by Weismann was based chiefly on zoological evidence. The early segregation of the germ-cells in the animal body weighed greatly with him. But it needs to be stated that in Plants early segregation does not occur. In them the tissues, still undifferentiated as somatic and germ-cells, are for long exposed to whatever the conditions of life may be before the gametes are specialised. This suggests that Plants would be particularly favourable subjects for observation in testing this question.

Mendelian Segregation.

It had long been known that offspring produced by the crossing of closely related forms, whether of Animals or Plants, does not always come true to type. But it remained for Mendel to discover the laws, since verified by many observers, which operate in the distribution of the characters of the parent forms among the offspring. The following description of one sample of Mendel's experiments is based, with Professor Punnett's permission, upon passages in his book on Mendelism.

In the selection of a plant for experiment Mendel recognised that two conditions must be fulfilled. In the first place the plant must possess differentiating characters, and secondly, the hybrids must be protected from the influence of foreign pollen during the flowering period. In *Pisum sativum* Mendel found an almost ideal plant to work with. The separate flowers are self-fertilising, whilst complications from insect-interference are practically non-existent. There are numerous varieties of the eating-pea exhibiting characters to which they breed true. Mendel selected a certain number of such differentiating characters, and investigated their inheritance separately for each character. Thus in one series of experiments he concentrated his attention on the stature of the plants. Crosses were made between tall and dwarf varieties, which previous experience had shown to come true to type with regard to these characters. It mattered not which was the pollen-producing, and which the seed-bearing plant. In every case the result was the same. Tall plants resulted from the cross. For this reason Mendel applied the terms *dominant* and *recessive* to the tall and dwarf habits respectively. Seeds collected from the first cross (F1), and sown the following year, gave both tall and dwarf plants among the offspring. Each individual was either tall or dwarf, and no intermediates appeared. In one series of experiments Mendel obtained 1064 plants, of which 787 were tall and 277 were dwarfs. That is, the dominant and recessive characters occur in the second generation of hybrids (F2) in the proportion of 3 : 1.

In the following year seeds from this generation (F2) were sown as before, and produced F3 generation. From the seeds of the dwarfs came only dwarfs, *i.e.* the recessive character bred true. The tall plants, however, of the F2 generation were not all of the same nature. Some of them produced seed which gave rise to tall plants only. Others formed seed from which sprang both talls and dwarfs in the proportion of 3 : 1. The tall plants of the F2 generation thus proved to be of two kinds, viz. those which carried only the tall character, and those which carried both tall and dwarf characters. The former are called "pure," and the latter "impure" dominants. By observations on F3, and subsequent generations, Mendel showed that the pure dominants and recessives always bred true, resembling in this way the original parents. The impure dominants, on the other hand, always gave dominants and recessives in the constant ratio of 3 : 1. Since the pure dominants are only half as numerous as the impure dominants, it follows that the impure dominant, on being self-fertilised, produces as offspring pure dominants, impure dominants, and recessives in the proportion of 1 : 2 : 1. The case of only one pair of characters has been considered here, but Mendel showed that the rule holds good for all the various pairs of differentiating characters studied by him; and since his time his conclusions have been verified in numerous instances both in Animals and Plants.

A general scheme may be constructed showing the result of crossing individuals which each bear one of a pair of differentiating characters. If D represent the pure dominant; and the impure dominant, which cannot be distinguished from it by appearance, be represented by (D); and if R represent the recessive, then the following will be the scheme of inheritance:

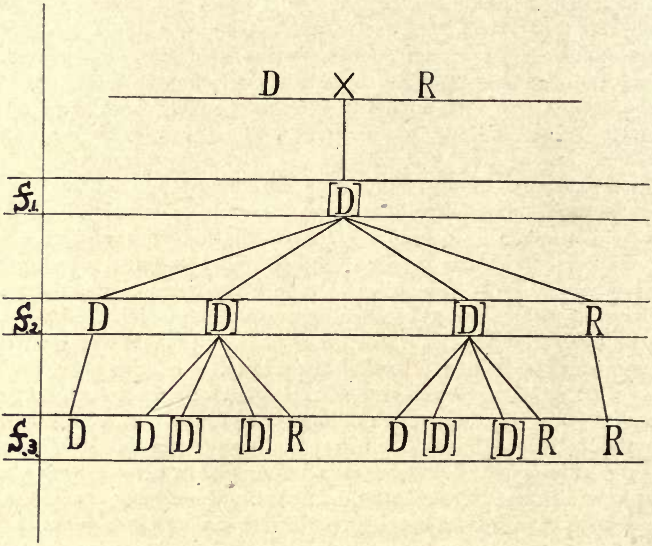


FIG. 395.

Scheme of inheritance of Dominant, D, and Recessive, R, characters resulting from the crossing of individuals which each bear one of a pair of differentiating characters, through three generations f_1, f_2, f_3. (After Punnett.)

In this scheme two pure strains, D, R, each possessing one of a pair of differentiating characters, are crossed together. The resulting hybrids, F1, all resemble the dominant parent. When self-fertilised they give offspring F2, of which one quarter bear the recessive, and three quarters the dominant character. Of the latter, however, only one-third are pure dominants, giving when self-fertilised, offspring in which the dominant character alone appears. The remaining two-thirds are impure dominants, which on self-fertilisation behave as the original F1 hybrids, yielding pure dominants, impure dominants, and recessives in the proportions 1 : 2 : 1. This is true for all impure dominants, no matter in which generation they occur. *Both the "extracted" pure dominants and the "extracted" pure recessives, which are formed in any generation after a cross, breed true to the types of the original parents used in the cross.*

In any sexually reproduced organism the gametes form the link between successive adult generations. The characters peculiar to the adult must therefore be represented in their constitution. In the tall Pea some at least of the gametes, whether male or female, must carry the tall character: for from an impure tall three quarters of the offspring are tall. If the strain of tall Peas proves experimentally to be pure for that character, all the gametes must bear that character, and that alone. The union of two such gametes will give a zygote having the tall character only. Such a zygote is known as a *homozygote*. But a zygote formed by the union of two dissimilar gametes,—*e.g.* in the case of Peas where one bears the tall and the other the dwarf character,—is termed a *heterozygote*. The plant produced from a heterozygote frequently shows the form of the pure dominant, and can only be distinguished from it by the test of breeding. That the recessive character is carried by it is shown when such heterozygotes are bred together: one quarter of their offspring prove then recessive. Such facts led Mendel to the conception of *pairs of unit-characters, of which either can be carried by any gamete to the exclusion of the other.* A fundamental property of the gamete is that it can bear either one of such characters, but not both of them. The heterozygote is formed by the union of two dissimilar gametes, and consequently the cells of the individual into which it grows must contain both characters. To reconcile these statements it must be supposed that at some cell-division in the formation of gametes a primitive germ-cell divides into two dissimilar portions. Instead of the dominant and recessive constituents passing in combination to the two daughter-cells, the whole of the dominant goes into one of these, and the whole of the recessive into the other. From this it follows that every gamete contains only one of such pair of characters, *i.e.* it is pure for that character. In other words, *a simple heterozygote produces gametes of two kinds, and produces them in equal numbers. The characters are said to* SEGREGATE *in the gametes.*

If we now return to the details of the tetrad-division described above (pp. 466-470), it is seen that the segregation postulated as the result of Mendel's experiments is actually effected in the reduction-division, which precedes the formation of gametes. Nuclei of two types are there segregated, each tetrad having two of each type. From the cells containing these nuclei the gametes which share their characters are finally derived. *Two types of gametes are thus produced, as the Mendelian experiments require for their explanation.* The results arrived at first by the actual experiments in crossing, and thereafter explained on the basis of the nuclear details, will be made clear by Professor Punnett's figure (Fig. 396).

The zygotes are represented by squares, the gametes by circles. Every zygote, being formed by fusion of two gametes, is double, and contains two factors belonging to a pair of characters. These factors are represented by rectangles, the recessive being black. As applied to the Peas of Mendel's experiment, the original parents (P1) are pure tall and pure dwarf, the latter being the pollen-parent. In (F1) the heterozygote contains factors of both tallness and dwarfness, but the plants are all tall like the tall parent. The factors being unsplittable, on producing gametes these plants yield equal numbers of two sorts, bearing tall and dwarf factors respectively. Every ovule which bears the factor for tallness has an equal chance of being fertilised by a "tall" or a "dwarf" pollen-grain, and "tall" ovules will therefore give rise to equal numbers of homozygous and heterozygous talls. Similarly with "dwarf" ovules. Hence of every four zygotes in (F2), one will be

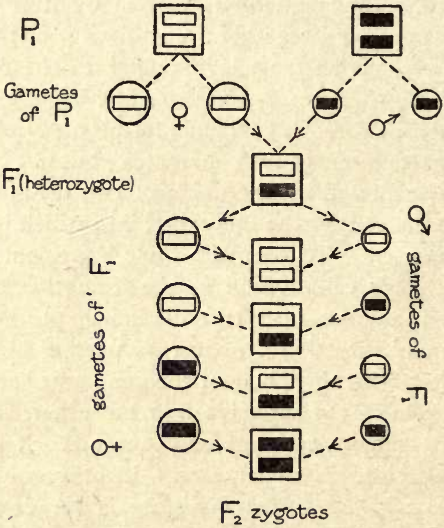


FIG. 396.
Scheme illustrating the segregation of characters of a heterozygote in tetrad division. See Text. (After Punnett.)

homozygous for tallness, another homozygous for shortness, and the remaining two heterozygous. These conditions, which correspond to the number resulting from experiments, are represented by the middle column of the (F2) zygotes.

Since by Mendelian segregation the racial characters are thus being constantly sifted out, and kept pure, one chief effect of sex upon heredity will be *the perpetuation of new heritable characters.* A plant resulting from a mutation would be liable to interbreed with the more numerous normal forms. There would thus be a probability of the mutation being swamped by promiscuous crossing, were it not for the fact that the segregation will tend in each generation to sift the pure heritable mutation out again. An innovation will thus be indestructible, provided it be not injurious. If it is injurious it will be eliminated by Natural Selection. *The effect will be the survival of harmless or beneficial mutations.* In the case of hybrids this appears in the tendency they show to revert to one of the original forms. In practice Mendelian segregation has already been used in the establishment of pure varieties of cultivated plants resistant to disease, and conspicuously in the case of Wheats. But the practical application of Mendelian methods is still in its infancy, and will probably be slow, because of the extreme complexity of the questions which arise, except in the simplest cases.

Sexuality appears to bring as a consequence the distribution and perpetuation of inheritable characters. Mendelian segregation is not in itself a constructive process. It is a distributive agency. Attention will then be centred not on the agency, however interesting and impressive its working may be, but upon the origin of the factors which it distributes. *The central question of Evolution comes finally to be the origin of the Heritable Mutations.* Of this as little is positively known at the moment as of the constitution of the protoplasm that gives rise to them.

Irregular Propagation.

Some Plants may eliminate normal sexual propagation, substituting for it in various ways other means of increase in numbers. Thus they forego the advantages which follow from sexuality, but not unfrequently they secure greater certainty of propagation. The commonest cases are where vegetative propagation replaces partially or completely the reproduction by seed : a condition common in Nature, and seen in special degree in cultivated plants, such as the Potato, Jerusalem Artichoke, Sugar-Cane, Banana, and Pine-Apple (Chapter XII.). In the viviparous habit of Alpine Plants the substitution of vegetative buds for flowers is probably a biological accommodation to the shortness of the Alpine summer. Frequently, however, there may be an apparent maturing of good seeds, though the embryos within them are not sexually produced. In *Funkia*, *Coelebogyne*, and others, numerous embryos arise by adventitious budding from the tissue of the nucellus, and they project like normally produced embryos into the embryo-sac. The nucellar tissue in such cases was already diploid : so that here there is neither reduction nor sexual fusion. They are peculiar examples of sporophytic budding. But as they involve a loss of sexuality, they may be described under the general term of *Apogamy*, or better, of *Apomixis*, by which is meant quite generally the absence of syngamy where it would normally occur.

Somewhat similar states, which however involve the contents of the embryo-sac, are found in *Alchemilla*, *Thalictrum*, *Taraxacum*, and *Hieracium*. In them embryos may be formed from an ovum without fertilisation. But here the egg itself has been found to be diploid, for reduction had been omitted in the development of the embryo-sac. Technically this has been described as "*somatic parthenogenesis,*" which implies that the embryo springs from the ovum, but the ovum was itself diploid. A like condition has been seen in *Marsilia Drummondi*, and in *Athyrium filix-foemina*, var. *clarissima*. In such cases again no fertilisation is necessary to arrive at the diploid state. A more rare condition is that where an egg that is really haploid develops as though it had been fertilised. This is not known in Seed-Plants, but it has been found to occur in *Chara crinita*. It is described as "*generative parthenogenesis.*"

Contrasted with these cases of apomixis, where no sexual fusion occurs, are various conditions which may be ranked as *substituted sexuality*. Here a nuclear fusion is seen, with consequences like those following on normal syngamy. But the nuclei involved are not produced in the normal way. Examples have already been described for *Nephrodium pseudo-mas*, var. *polydactylum* (p. 350, Fig. 294); and in that unusual type of nuclear association which occurs in the formation of the fruit in the Uredineae (p. 448, Fig. 384). In the latter the association is ultimately followed by nuclear fusion, which thus, though deferred, takes its place in the cycle. The fact that similar nuclear fusions precede the formation of ascospores (p. 430) and of basidiospores (p. 441) suggests that such methods are probably wide-spread among Fungi. The nuclei involved in such cases spring not from any widely distinct sources, but from cells closely related in position and in origin. It is remarkable that these and other irregularities in the sexual cycle are found commonly among Plants represented by very numerous closely related forms. If their numerous species and varieties have resulted from mutation, then it would appear that excessive mutation may have had some influence in producing those irregularities. In organisms which show mutation freely, the Mendelian sifting out, and preservation of each heritable mutation, would be a less vital matter than it is in more stable forms. This may in some degree account for such deviations from the normal sexual reproduction as have just been described.

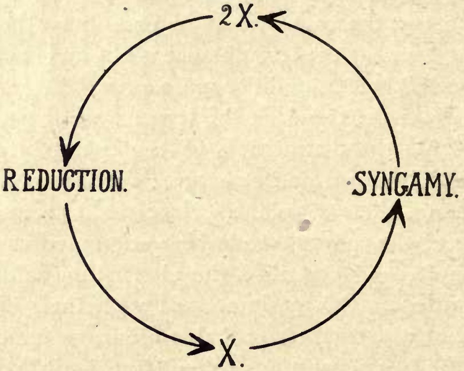
CHAPTER XXXII.

ALTERNATION OF GENERATIONS, AND THE LAND-HABIT.

THE expression "Alternation of Generations" was brought into prominence by Steenstrup, who applied it to the succession of phases in the life-history of Medusae, Trematodes, and other Animals. He defined it as "the remarkable natural phenomenon of an Animal producing an offspring which at no time resembles its parent; but which itself brings forth a progeny which returns in its form and nature to the parent Animal." The publication of Steenstrup's essay preceded the demonstration by Hofmeister of the life-history of Mosses, Ferns, and Conifers. These researches disclosed phenomena of Alternation in Plants superficially so like those in Animals that it was natural to use the same terms in describing them. But later it has become clear that the resemblance is not an exact one, and that the "generations" in Plants differ more essentially from one another than those in Animals, to which the terms were originally applied.

In many Plants the distinctness of the sporophyte and gametophyte is marked by form and structure; for instance, that between the prothallus and the Fern-plant. Nevertheless some contemplated the possibility of the sporophyte having originated as a modification of a gametophyte, and described the alternation as one of "homologous" generations. Others, impressed with their distinctness not only in form but also in their probable origin as indicated by comparison, held the two generations to be "antithetic," that is, distinct in their origin and history from one another. The discussion of the question seemed likely to pass into an inconclusive dialectic, when a fresh point was given to it by the discovery that in Plants there is a prevalent nuclear difference between the two generations. In such Plants as may be held to be normal, the sporophyte was found to have diploid nuclei, and the gametophyte nuclei that are haploid. This distinction is not matched by any corresponding known difference in Animals, in which the whole body appears to be consistently diploid. Thus while Botanists have assumed the term "Alternation of Generations" first used in relation to Animals, they now apply it to a phenomenon in Plants which proves to be peculiar to them. The descriptions already given of the life-histories of Plants have provided many facts which may now be drawn together into a comprehensive statement on Alternation, and on the changes and modifications which it shows in relation to habit.

In normal Plant-Organisms which show sexuality the fusion of two nuclei in syngamy has been found to result in a doubling of the number of chromosomes in the zygote. This has been demonstrated in so many well-authenticated cases that it may be held as a general consequence. At some other point in their life-cycle, and always before another sexual fusion occurs, there is a tetrad-division, which results in the reduction of the number of chromosomes again to one half. The second process may be held to be complementary to the first, and it appears to be necessary if the number of chromosomes is to be kept within limits after successive generations. The life-cycle in sexually propagated plants is thus made up of two phases: the one intervenes between syngamy and reduction, and is *diploid*, *i.e.* with $2x$ chromosomes. It is commonly styled the *sporophyte*, or non-



sexual generation, because it usually terminates in the production of non-sexual spores. These *spores* are consequent on a tetrad-division, and may be styled specifically *carpospores*. The other is *haploid*, *i.e.* with x chromosomes. It is commonly styled the *gametophyte*, or sexual generation, because it normally results in the formation of *gametes*. The cycle thus constructed may be represented as in the diagram given above. Since the two phases follow one another in regular succession, this phenomenon is that which is now understood as the normal *Alternation of Generations* in Plants.

It seems probable in many, though not perhaps in all phyla, that nuclear fusion and reduction remained constant features in each completed life-cycle throughout Descent. In that case two opportunities for somatic amplification were possible in Evolution from simpler forms. The one between syngamy and reduction would give rise to the body of tissue called the sporophyte. The other between reduction and syngamy would give rise to the gametophyte. If the fusion and reduction retained their identity throughout descent, these two somata can never have been homologous, that is, homogenetic by descent. They must have been "antithetic" throughout, however nearly they may resemble one another in their characters. If they both develop in the same medium, they being in fact merely phases of the same organism might be expected to resemble one another very closely. That is found to be actually the case in many Algae and Fungi. For instance, in *Dictyota* among the Brown Algae, and *Polysiphonia* among the Red, the two generations appear identical; they seem only to differ in their chromosome-number, and in the propagative organs which they bear. Similarly in the Uredinae (p. 449), the paired nuclei of the sporophyte on the Wheat are contained in hyphae similar in their main features to those of the gametophyte on the Barberry, which have only single nuclei. Much the same is the case in those Ascomycetes in which evidence of alternation may be traced. There may be a difference of potentiality between the haploid and diploid phases; but it need not be realised where the circumstances are uniform, as when both grow in water, or in moist conditions. In that case both may appear alike.

Alternation in Thallophytes.

The cytological data for the Thallophytes are still so imperfectly known that all comprehensive statements as to alternation in them must be provisional. They probably represent a large number of phyletic lines. In those which show sexuality the life-cycle appears to have been subject to the twc alternating events of syngamy and reduction, but to have been worked out in various ways in respect of somatic development in relation to them. A few examples will be cited as showing how various the results have been. A very simple but instructive case is that of the Diatoms and Desmids. In the Diatom, *Rhopalodia*, it has been shown that a tetrad-division of nuclei *precedes* conjugation. In the Desmid, *Closterium*, a tetrad-division *succeeds* conjugation. If, as is probable, reduction is the consequence of that tetrad-division, then the cell of *Rhopalodia* would be diploid throughout its vegetative divisions; but that of *Closterium* would be haploid. On the chromosome-definition such Diatoms would represent the sporophyte-generation, but the very similar Desmids the gametophyte (p. 401).

In larger Algae the position of the event of reduction in the life-cycle is seen to vary even in organisms that are related to one another. Thus among the Brown Algae, *Dictyota* has distinct though similarly formed and alternating sexual and tetrasporic plants, the former with 16, the latter with 32 chromosomes. Here reduction accompanies the formation of tetraspores (p. 387). But in *Fucus* there are no tetraspores, and reduction takes place *before* fertilisation, in the first divisions respectively of the oogonium and antheridium. The doubling of them in fertilisation results on germination directly in the *Fucus*-plant, which is accordingly *diploid*. There is here no alternation of distinct diploid and haploid generations. In the Red Seaweeds the converse is the case. The relatively simple Nemalionales have been shown to carry out reduction immediately *after* fertilisation. Here again there is no alternation of generations, and the plant as such is *haploid*. But most of the Red Seaweeds have alternating generations, the one haploid, bearing gametes (gametophyte), the other diploid, bearing tetraspores (sporophyte) (p. 389). Such a life-history corresponds to what is seen in *Dictyota*. But when we compare the Nemalionales with *Fucus* we see that the former are haploid, the latter diploid. The difference between them is the same as that already noted between *Closterium* and *Rhopalodia*. It appears then that Algae may be (i) haploid without any distinct alternation (*Closterium*, Nemalionales); (ii) diploid without any distinct alternation (*Rhopalodia*, *Fucus*); or (iii) with distinct alternation of generations (*Dictyota*, *Polysiphonia*, and other Red Seaweeds). In all of these there is only one constant feature, the alternation of syngamy and reduction. Those events may follow in quick succession, or they may be separated by intervening somatic developments.

It has been suggested as probable that the simpler condition, with only one generation, as seen for instance in the Nemalionales, is more primitive than that with two, as in *Polysiphonia*. In explanation how the latter may have come into existence two alternatives appear possible. Either an interpolation of a sporophyte by successive steps, or a sudden deferring of reduction. In the latter case it is possible to imagine a carrying over of the reducing act to a later phase of the individual life. It has been suggested that the unicellular spores (monospores) already known in the Nemalionales, may have been in other Red Seaweeds converted into tetraspores by some sudden deferring of the act of reduction. A final judgment on this question must be held over till the necessary comparisons with allied forms shall have been made. But meanwhile the fact that in certain Ferns the stage externally that of the "gametophyte" may be diploid (*Athyrium filix-foemina*, var. *clarissima*), and the stage externally that of a sporophyte haploid (*Lastraea pseudo-mas*, var. *cristata*), would seem to indicate the possibility of the suggestion being true (p. 350).

The whole series of facts of alternation in the Thallophytes suggests that the relative uniformity of the conditions, under which these successive phases grow, has operated so as to stamp a high degree of uniformity upon the somatic developments included in their life-cycle. The only constant rule seems to be that doubling and reduction of chromosomes should regularly succeed one another. It is otherwise, however, in organisms which grow under less uniform conditions. In them the alternation of the two somatic phases becomes more definitely stamped by difference of form, as it is seen to be in the land-living Archegoniatae.

The Land Habit.

No circumstance of Life has more profoundly affected Organic Evolution than the progression from water to land. The further the comparative study of the simpler living beings is carried, the more the conclusion is confirmed that the birth-place of Animals and Plants was in the water. The comparative study of the Higher Animals and Plants demonstrates as fully that it is in sub-aerial conditions that both have reached their highest development. Accordingly it becomes a question of supreme interest what are the effects impressed upon the organism by a Land-habit in place of its original aquatic surroundings. Certain factors stand out clearly. First, the mechanical requirement for support and maintenance of form. The body, whether of Animal or Plant, is nearly of the specific gravity of water. When immersed it is buoyed up, and provided the water be not itself in violent motion there is little demand on the organism for mechanical resistance. It is different, however, with sub-aerial organisms, which require not only to support their own weight in the lighter medium of air, but they must also maintain their form under the stress of winds, and other strains incident to life on land. The larger the organism the higher still will be the *ratio* of the demand. Such questions of mechanical strength have been taken up for Plants in Chapter IX., and need not be discussed again here. A second factor is the need for protection of the protoplast against loss of water by evaporation. The evidence of its importance is seen in the very general presence of a cuticularised wall covering all the exposed surfaces, as well as in the simple fact that no Land-living Plant sheds its *ova* from the parent, as so many Algae do. A third factor is the need for internal aeration of the tissues wherever they assume large bulk. Another which has contributed to the moulding of Plant-Organisms living on land is the requirement of a large surface of exposure to light and air for Photo-Synthesis. Such factors as these must be considered in their effect on the Evolution of Organisms showing sexuality and alternation, as they adapted themselves to a Land-habit.

It is not known from what source the Land-Vegetation sprang.

Presumably it was from some Algal ancestry in which sexuality was already established, and perhaps it already possessed a definite alternation of generations. It cannot be asserted what the balance of those generations was. But judging from the constancy of well-marked alternation of x and $2x$ generations in all land-living forms, and the fact that such alternation is also present in Algae, both generations may have been already in existence as somatic structures before the transition to Land-Life. This, however, appears to have fixed, and indeed differentiated the two generations: so that the Bryophyta and Pteridophyta now appear as the headquarters of well-marked alternation of generations with distinctive characters of form and structure.

A most important feature of the Land-Vegetation is the *retention of the ovum* within the parent plant. It is enveloped in the archegonium. The archegonium itself is so constant in the earlier Land-Vegetation that on it is based the name "Archegoniatae," so often applied collectively to the Mosses and Ferns. The explanation of its constancy of form and structure, though not of segmentation, is to be found in the imperative need for the protection which it offers to the ovum, but without excluding access of the spermatozoid at the receptive period. The immediate consequences of this retention of the ovum are seen in the fact that Archegoniate Plants, or their Gymnospermic derivatives, form the bulk of the early Fossil Flora, and are an integral part of the Land-Flora of the present day. But such organisms have not cut themselves wholly adrift from their original mode of life. They are still dependent upon external fluid water for the fertilising act itself, since it is through water that the male gamete moves to the egg. Moreover, the gametophyte with its relatively delicate structure is essentially dependent upon moist conditions for its normal growth.

Rise and Decadence of the Gametophyte.

The gametophyte has never made a real success of Life on Land, as measured by size and structure. But this in itself makes the study of its partial success the more interesting. In Ferns and the thalloid Liverworts it is commonly a flattened thin or fleshy body of undifferentiated tissue, capable of self-nourishment and absorption from the soil. In extreme cases, growing in very moist and shaded conditions, it may be even filamentous, while the Alga-like habit is accentuated by vegetative propagation by gemmae. The thalloid

Liverworts also show this ; but in their larger forms the upper surface of the thallus may be alveolated, and the cavities occupied by Photosynthetic tissue, so as to make them efficient for self-nutrition in dry air, as in the leaves of Flowering Plants (p. 365). In the Mosses and leafy Liverworts, after a preliminary filamentous stage, a leafy plant is formed after the fashion of the leafy sporophyte. In the larger forms it may develop a conducting system, while sometimes, by involution of their surface, its leaves may acquire a structure efficient for Photo-Synthesis combined with water-control (p. 357, 358). But the size of these gametophytes is never great, and often very minute. Even in its most successful forms the sexual generation suffers from the disability of an absence of internal ventilation. Air-containing intercellular spaces are wanting. The plant is essentially semi-aquatic, and often saves itself in its land-habitat, as the Mosses do, by its power of dormant vitality under drought, and its readiness of surface-absorption whenever water is available. Thus constituted the gametophyte is a constant menace to success of the Archegoniatae, as Land-living Plants. Its delicate structure, and, finally, its dependence on external fluid water for fertilisation, have tended to tie the lower Archegoniatae down to limited habitats, from which they have never been fully emancipated.

Some of the most archaic plants that have survived, such as the Psilotaceae, Lycopods, and Ophioglossaceae, have underground prothalli with endotrophic mycorhiza, and saprophytic nutrition (Chapter XI.). It must suffice here to note the fact without detailed description. In view of the disabilities of the gametophyte for life on land, the underground habit, and the form of saprophytic nutrition which these plants possess, may well have been conditions which have determined their survival.

The difficulty presented by this dependence of the gametophyte upon external water has been met in the Higher Flowering Plants by a repetition of the method already so successful in the first conquest of the Land, viz. the *retention of the vulnerable part upon the parent.* First the ovum was retained, as in the Archegoniatae, then the whole prothallus which bears it, as in the Seed-bearing Plants. For this the way was prepared by the sexual differentiation of the spores. Within each of the phyla of Ferns, Lycopods, and Equiseta, this differentiation has taken place. In each case the original state was, as in all the Bryophytes, *homosporous*, with all the spores alike, and commonly yielding on germination a bi-sexual prothallus (p. 342, Fig. 388). The first step is a separation of the sexes on distinct prothalli. A purely male prothallus has no permanent duty, but only the temporary function of producing spermatozoids. It may therefore, and it does, remain small. But the female prothallus has both to produce ova and to nourish the embryo after fertilisation. This can best be carried out by a large prothallus, which will develop better from a well-nourished spore. This is the physiological *rationale* of the origin of the megaspore as distinct from the microspore, as seen in *Selaginella*, which is heterosporous (p. 320). The same condition is also seen in certain Ferns (*Marsilia*, *Azolla*), and in many fossil Lycopods and Equiseta. But still the megaspore in these plants is shed from the parent before fertilisation, and is then dependent on its own resources. The longer the period of connection with the parent the better. *A further advantage was then gained by retention of the megaspore itself upon the parent plant until the embryo is far advanced.* The sporangium which thus retains its megaspore is called an *ovule*, and this matures into the *seed*, which is characteristic of all the Higher Plants of the Land (p. 283). The prevalence of the Seed-habit is the token of its success.

While a certainty of protection of the prothallus, and of continued nutrition of the embryo is thus secured by retention of the megaspore, or embryo-sac, upon the parent, the steps of progress involved have reacted adversely upon the gametophyte generation. The separation of the sexes tended to relieve it of the necessity for self-nutrition. Provided the microspores are numerous, and each has a sufficiency of material to form an antheridium and spermatozoids, that would meet the requirements, and little or no vegetative tissue is needed. This condition is characteristic of heterosporous plants. It is seen in *Selaginella* (p. 321, Fig. 264), and in the pollen of Gymnosperms and Angiosperms with their vestigial male prothalli (Figs. 194, 251). On the other hand, the megaspore requires to be well nourished, in the interest of the archegonia, and the embryo which it is to bear. But it receives its supply from the parent plant, rather than by its own self-nutrition. Thus in the case of a megaspore of *Selaginella* the female prothallus is little more than a storage tissue, and a basis for archegonia (Fig. 265). Self-nutrition is reduced, or entirely absent as in the Gymnosperms; and, finally, in the Angiosperms the female gametophyte is so transformed that it is difficult to homologise the contents of the embryo-sac at all with a female prothallus.

The spermatozoid motile in water remained, however, as the means of fertilisation even after the adoption of the Seed-habit. It is still seen in the Ginkgoaceae and the Cycads, though its unpractical nature is evident (p. 315). The last step of emancipation from the original aquatic method of propagation was the substitution of the motile spermatozoid by the non-motile gamete delivered by the pollen-tube (Figs. 213, 214). Thus the most critical point of each life-cycle, viz. fertilisation, was finally adapted to Life on Land. And so by a series of steps the gametophyte is reduced, altered, and in some cases almost obliterated. It has paid the penalty of its inability to adapt itself thoroughly to sub-aerial conditions. The climax of the gametophyte on land is attained in the homosporous Mosses and the leafy Liverworts. It appears of independent, though limited growth in the homosporous Ferns. But with heterospory it fades into insignificance, and in the Higher Seed-Plants it survives as a mere relic.

Rise of the Sporophyte.

The sporophyte, on the other hand, is seen in the ascendant in the progressive series of Land-living Plants. By adaptation of form and structure it has met, in its highest terms successfully, the requirements for mechanical strength, for protection under drought, for exposure of a large surface for Photo-Synthesis, and for ventilation of extensive nutritional tissues. In all these respects it is the superior of the gametophyte, and perhaps the structural feature that has contributed most to its supremacy is the ventilation-system of intercellular spaces, controlled by stomata at their exits to the open air. This differentiates the sporophyte from the gametophyte more clearly than any other structural character, and stamps it as adapted to sub-aerial life. *The end of its vegetative existence is the formation of spores (carpospores).* The more numerous these are (other things being equal) the better the chance of survival of the species, and of its spread. The vegetative development may be regarded as a means to that end, and in homosporous forms its nutritive capacity imposes the only limit on spore-numbers. The dispersal of the spores is dependent in primitive land-forms upon a dry atmosphere. This is in strong antithesis to the necessity for external fluid water for fertilisation, which is the end of their gametophyte. The apparent steps in elaboration of the sporophyte, and in its specialisation for the certain establishment of germs under sub-aerial conditions may now be briefly sketched, the illustrations being drawn as far as possible from organisms described in previous chapters.

The origin of the sporophyte in the Archegoniatae is quite problematical, since no certain ancestry is known for them. It has been suggested on the one hand that the dependence of the sporophyte upon the gametophyte is a true indication of its derivative origin. In that case the sporophyte may have originated from a post-sexual production of spores, and have been originally without vegetative tissue: the latter being produced in the first instance by STERILISATION of some of the potential spore-mother-cells. Comparison among the sporogonia of Liverworts and Mosses makes it appear probable that such sterilisation has actually occurred in them. On this theory the simple sporogonium of *Riccia* (Fig. 313), which has no distinction of apex and base, would represent a primitive state, and more elaborate capsules may be seriated progressively in relation to it.

A good case can be made out for an alternative view: that the Archegoniatae sprang from some Algal ancestry which already possessed alternate but separate generations, of which the sporophyte developed from a freely shed ovum. That on adopting a land-habit the ovum, ancestrally fertilised as it lay free in the water, was retained on the parent gametophyte, in a protective organ, the archegonium; and that the ENCAPSULATION had its effect in moulding and modifying the young sporophyte to such forms as are seen in the simpler Bryophytes. In the present state of actual knowledge such suggestions are little better than speculations.

The sporogonium of the Bryophyta is usually held to represent the most primitive type of sporophyte among Land-living Plants, and recent discoveries of very early fossils tend to support that opinion. Its limited plan of construction, and its ephemeral character, the absence of appendages, the preponderance of spore-production, and its dependence throughout life upon the gametophyte, are all indications pointing in the same direction. The fact that the spore-production is simultaneous in each sporogonium, and that it arises from one undivided sporogenous tissue, not from a number of distinct sporangia, also points to the same conclusion. Within the Bryophyta the various forms may be seriated so as to give probable indications of progressive advance in various important characters. These suggest that from a very primitive spherical type, such as *Riccia* (Fig. 313), apex and base were first defined. A sterile stalk and central columella were acquired, and later, specialised methods of spore-distribution. These rose to high efficiency in the higher Mosses (Fig. 296). Incidentally, parts of the tissue of the more complex forms assumed a Photo-synthetic function. A well-formed epidermis and stomata are found in some of them, while beneath this lie assimilating tissues as well ventilated as in the leaves of Vascular Plants (Fig. 305). Nevertheless the simple form, the limited apical growth, the absence of appendages, and above all the want of any direct connection with the soil, stamp even the most elaborate sporogonium as an only partially efficient structure. To achieve higher development it would be necessary to break away from so restricted a plan, which in itself is only practically possible where the gametophyte shows high elaboration, so as to supply the nourishment the sporophyte cannot wholly acquire for itself.

In various ways the Homosporous Pteridophytes show the result of such emancipation, and they may perhaps have originated from some source like the sporogonium seen in certain Bryophyta. The features in which they show superiority to these as spore-producing plants are (i) an unlimited capacity for apical growth; (ii) the possession of lateral appendages; (iii) a direct access to the soil by a root-system; (iv) an improved conducting system; (v) a greatly elaborated Photo-synthetic system, partly dependent on external form, partly on more complete differentiation of vegetative from propagative regions of the plant; (vi) the formation of numerous distinct sporangia; and (vii) the production of the sporangia not simultaneously, but in succession, or even delayed, so as to spread the physiological drain over a long period. Possessed of these features the sporophyte develops as an independent, self-nourishing organism, unlimited in plan, in period of life, and in power of spore-production. It is the sphere of Special Morphology to trace the lines along which these various features have probably been acquired. But the result of them is seen in varying proportion and efficiency in any ordinary Fern, or Lycopod, or Horsetail. These are characteristic examples of the primitive Vascular Plants of the Land. They depend upon the vegetative development of a freely-rooted sporophyte for their legitimate success, while still retaining their *Homosporous state*. In point of size the acme of achievement of the Homosporous Pteridophytes now living is to be found in the Filicales; though they still show for the most part a leafy shoot which serves general purposes, and is not strongly differentiated into vegetative and propagative regions.

It was the adoption of the *Heterosporous state* and the retention of the female spore and its prothallus within the megasporangium or ovule, that paved the way for the full possession of the Land by a Seed-bearing Flora. Plants thus finally broke away from the physiological tie to external water for their fertilisation. Seed-production is carried on in a compact *Strobilus*, or *Flower*. Evidence of the steps of segregation of the "general purposes shoot" into distinct nutritive and propagative regions may still be traced in favourable cases (see p. 241). These regions once established took each its own independent line of specialisation in the evolution of Seed-bearing Plants. The vegetative region which appears first in the individual life commonly develops normal foliage; but under special conditions it may become xerophytic, scandent, parasitic, or saprophytic, suiting its form to the circumstances (Chapters X., XI.). The propagative region or Flower also became specialised in relation to its functions. It appears later, and is distal, since nutrition is necessary before propagation can be carried out. This distal position, while it is further removed from the water-supply, offers the best opportunity for transfer of pollen, whether by wind, or by animal agency. The functions of the Flower are, to produce sporangia; by its structure to offer facilities for pollination, with fertilisation as its consequence; to protect and nurse the new germs up to the period of ripeness of the seed; and, finally, to secure seed-dispersal. The means by which these ends are attained are almost infinitely various. Examples are described at length in Appendix A. It is the high degree of adaptability of the Seed-bearing Plants to sub-aerial conditions, so as to secure these ends, that has given them their supremacy. The pollen-grains, usually dry and dusty, retain essentially the character of the micro-spores of the Pteridophyta. They thus allow of either self-pollination, or of inter-crossing in various degrees, in organisms themselves non-motile. Commonly they are exposed at the time of flowering to dry air and full sunlight. The antheridial mother-cell within each grain is protected by the cuticularised and often coloured coat of the grain from injury by drought or intense light: its products are not set free into water as in the Amphibious Pteridophytes, but pass into the security of the pollen-tube: there the male gametes are formed, which are passed on to their destination as the tube grows (Chapter XVI.). Similarly, the ovum is never exposed. Its protection against all risks is secured by a succession of tissue-envelopes. The carpel, one or two integuments, and finally the nucellus all take their part in this duty. The ovum itself, a primordial cell not differing essentially from the exposed egg of *Fucus*, thus deeply sunk in living tissue, is immune to the risks of sub-aerial life. It is in a position, when fertilised, to draw its supplies during the nursing period from the embryo-sac, and the surrounding envelopes. Such conditions, combined with the effective and often elaborate means of distribution of the ripe seeds already described (Chapter XVIII.), account for the Seed-Plants becoming the chief factor in Land-Vegetation. The disabilities of the gametophyte for land-life have been evaded. The more adaptive sporophyte has developed specially so as to protect the most vulnerable points in the cycle of life, viz. the period of fertilisation, and the first stages of development of the embryo. *Thus the sporophyte has become virtually the Plant of the Land, and the gametophyte a mere vestige.*

A strong antithesis has been drawn between the relative failure of the gametophyte and the ultimate triumph of the sporophyte in subaerial life. The two generations differ normally in chromosome-number. This seems to suggest that a higher potentiality and initiative in variation lies with the diploid state. It may not be possible to lay it down as a general proposition that a double number of chromosomes is an index of greater power of adaptability; but it is a significant fact that the highest somatic evolution both in Animals and Plants has been attained by diploid, not by haploid tissues. The sporophyte is a non-sexual, or neutral generation, by nature and by origin. But the steps in obliteration of the gametophyte, and in the evolution of the seed, have involved the spread of the sex-difference backwards in the individual life, so as to affect the antecedent neutral generation. This will be apparent on comparison of the life-cycle of a homosporous Fern (Fig. 291, p. 348) with that of a Flowering Plant (Fig. 244, p. 299). The final culmination of this is found in those Seed-Plants which are diœcious, such as the Willow, or the Yew (Fig. 245, p. 300). In these some individuals bear only staminate, others only pistillate flowers, and the plants are thus ranked as "male" or "female": though in point of fact they represent the neutral generation. The end result is thus seemingly a parallel between the Higher Plants and the Higher Animals as regards sexuality. In both the individual appears to be either "male" or "female." But this similarity is superficial rather than real, for it has been attained along quite distinct evolutionary channels in the two Kingdoms. In the Higher Animals there is a true sex-difference between individuals, the one producing male, the other female gametes. In the Flowering Plants the individual is the neutral sporophyte, which does not itself produce gametes. But in the course of Descent certain distinctive features relating to sex have been reflected back from the sexual gametophyte which it ultimately bears, and comparison shows clearly the steps by which those features have been impressed upon the neutral Plant. Accordingly the Flowering Plant has secured such advantages as follow from sex, through its retention of the sexual generation within it. *Nevertheless the substantive Plant is actually the neutral generation, or Sporophyte, which is thus seen to have established its final ascendency in the Vegetation of the Land.*

APPENDIX A.

TYPES OF FLORAL CONSTRUCTION IN ANGIOSPERMS.

A description of a few types of Flower, together with notes on the Natural Families to which the Plants that bear them belong, are here added, so as to illustrate more fully the methods of floral construction described in Chapter XIII. They have been selected partly because they are common Flowering Plants easily accessible to all; partly because they represent characteristic features of the Natural Families whose products are of importance to Man; partly also because of their biological interest in relation to the production and dispersal of seeds. A study of such examples will give some idea of the various forms which the flowering shoot may assume. A few added notes will help to explain in the several examples the biological advantages which follow from the form adopted.

CONSPECTUS OF THE PLANTS DESCRIBED.

MONOCOTYLEDONEAE.

ORDER.	FAMILY.	EXAMPLES.
Liliales	Liliaceae	(1) Tulip, (2) Squill.
	Amaryllidaceae	(3) Snowdrop, (4) Pheasant's Eye.
	Iridaceae	(5) Iris, (6) Crocus.
Orchidales	Orchidaceae	(7) Orchis.
Glumales	Juncaceae	(8) Wood-Rush.
	Cyperaceae	(9) Cotton-Grass, (10) Sedge.
	Gramineae	(11) Rye-Grass.

DICOTYLEDONEAE.

(Dicotyledoneae—Choripetalae).

Salicales	Salicaceae	(12) Goat Willow.
Curvembryeae	Caryophyllaceae	(13) Ragged Robin, (14) Campion.

ORDER.	FAMILY.	EXAMPLES.
POLYCARPICAE	Ranunculaceae	(15) Marsh Marigold, (16) Buttercup, (17) Aconite.
RHOEADALES	Papaveraceae	(18) Poppy.
	Cruciferae	(19) Mustard, (20) Wallflower.
GERANIALES	Geraniaceae	(21) Geranium, (22) Pelargonium.
TRICOCCAE	Euphorbiaceae	(23) Spurge.
SAXIFRAGALES	Saxifragaceae	(24) Saxifrage, (25) Currant.
ROSALES	Rosaceae	(26) Apple, (27) Strawberry, (28) Rose, (29) Cherry.
LEGUMINALES	Leguminosae	(30) Trefoil, (31) Pea.
UMBELLALES	Umbelliferae	(32) Cow-Parsnip.

(DICOTYLEDONEAE—SYMPETALAE).

(*a*) *Pentacyclicae.*

BICORNES	Ericaceae	(33) Heath, (34) Bilberry.
PRIMULALES	Primulaceae	(35) Primrose.

(*b*) *Tetracyclicae.*

PERSONATAE	Solanaceae	(36) Nightshade, (37) Potato.
	Scrophulariaceae	(38) Figwort, (39) Speedwell.
VERBENALES	Labiatae	(40) Dead-Nettle, (41) Sage.
SYNANDRAE	Compositae	(42) Groundsel, (43) Ox-eye, (44) Centaury, (45) Dandelion.

MONOCOTYLEDONEAE.

These Plants are characterised by the embryo bearing only one cotyledon. The leaves are as a rule alternate, with simple form, parallel venation, and a broad sheathing base. The stem and root show no secondary thickening of the type usual in Dicotyledons, their vascular strands having no cambium. The flower is constructed usually of five alternating whorls of parts, and each whorl is commonly trimerous. Most of the Monocotyledons are perennials. They include Grasses, Sedges, Orchids, and Palms. Many are rhizomatous and bulbous plants that are grown for the beauty of their flowers.

ORDER: LILIALES.

The plants included in this Order are very naturally related, though their habit is not uniform. They are mostly perennials, with rhizomatous or bulbous stock; but sometimes they are tree-like (*Dracaena*), while some are climbers (*Smilax, Dioscorea*). They have long entire leaves, with a sheathing base, and parallel venation ; but the Dioscoreaceae are exceptional in having broad reticulate leaves.

The flowers are constructed on a type which may be accepted as a general underlying plan for Monocotyledons, being composed of five alternating whorls of parts. The number of parts in each whorl is commonly three ; but other numbers may be found, such as two (*Maianthemum*), or four, or even five (*Paris*, *Aspidistra*). The floral formula is P. $n+n$, And. $n+n$, Gyn. (n), and the floral diagram as in Fig. 397. The more primitive Liliiflorae have hypogynous flowers, but they are epigynous in the Amaryllidaceae and Iridaceae, a condition regarded as later and derivative. The ovary has one loculus for each carpel, and the anatropous ovules are seated on their incurved margins, which are fused to form an axile placenta (Fig. 399). The flowers are usually of large size, and are often conspicuous by colour and scent (Lily, Tulip). They show steps of progressive fitness for the nursing of the ovules, by various degrees of fusion of the carpels, and of sinking of the ovary from the superior position of the Liliaceae to the inferior of the Amaryllidaceae and Iridaceae. Progressive steps may also be traced in perfection of the pollination-mechanism.

FIG. 397.
General floral diagram for trimerous Flower of the Liliales.

Family: LILIACEAE. *Example:* THE TULIP.

(1) The Tulip plant (*Tulipa gesneriana*) at the flowering period consists of the underground bulb, bearing roots downwards from the margin of the disc-like stem, upon which the storage-scales of the bulb are seated. From its apex rises an elongated stem bearing a few foliage leaves, and a single terminal flower which is radially symmetrical. Provision for the next season is made by one or more buds in the axils of the bulb-scales, which grow into new bulbs, and each may produce a flower. Compare bulb of Hyacinth (Fig. 125, p. 166). The analysis of the flower is as follows :

Perianth segments 3 + 3, polyphyllous, inferior.
Androecium stamens 3 + 3, free, hypogynous.
Gynoecium carpels 3, syncarpous, superior. *Stigma* three-lobed, sessile. *Ovary* trilocular. *Placentation* axile. *Ovules* numerous, anatropous (Figs. 398, 399).

FIG. 398.
Superior gynoecium of *Lilium*, showing relative position of ovary (*ov*), style (*sty*), and stigma (*stig*).

The floral diagram (Fig. 397) shows the regular alternation of the successive whorls of three parts. As those of each whorl are all of equal size, and excepting the carpels all separate from one another, the Tulip may be held as a relatively primitive type of Liliaceous flower. But the syncarpous state here seen is probably not the most primitive. In *Colchicum*, with its Crocus-like habit, the carpels are incompletely fused, and each has its separate style and stigma: an indication of a primitive apocarpous state. Other members of the Order show various steps in cohesion and adhesion of the outer parts. For instance, in (2) the Wild Hyacinth (*Scilla nutans*, Sm.) the stamens are adherent to the perianth-segments (epiphyllous). In the Grape-Hyacinth (*Muscari*), and the Lily of the Valley (*Convallaria*) the segments of the perianth are coherent into a bell. In some Lilies the perianth may form a long tube, while the style is proportionally elongated. But still the ovary is *superior*; even in *Colchicum*, where it is below ground, it stands above the insertion of the long tube-like perianth. In others, as in *Hemerocallis*, the gamophyllous flower is zygomorphic. Thus the primitive state seen in the Tulip may be modified in relation to pollination by insects.

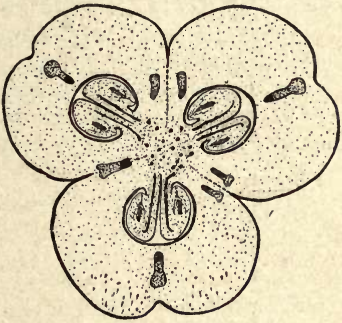


FIG. 399.
Transverse section of the superior ovary of Lily, showing the three syncarpous carpels, bearing the anatropous ovules on their infolded margins. F. O. B.

Pollination. The flower of the Tulip is conspicuous by its size and colour; but there is no honey, though in the nearly allied *Fritillaria* a large honey-gland lies at the base of each perianth-segment. The Tulip is visited by insects for its pollen and so crossing may be effected; but it is not a specialised mechanism.

The *fruit* of the Liliaceae is either a capsule, splitting by longitudinal slits, and so shedding the seeds, which are flattened, and readily carried by the wind; or it may be a berry as in Lily of the Valley, or Asparagus, and thus be distributed by birds.

Family: AMARYLLIDACEAE. *Examples:* SNOWDROP, NARCISSUS.

Those Liliales which have the same floral plan as the Liliaceae, but with an *ovary inferior*, are grouped as Amaryllidaceae. But there is no sharp line of demarcation between the hypogynous and the epigynous types. Some genera show an intermediate state, their half-inferior ovary suggesting how the carpels may have sunk into the tissue of the receptacle, thus giving the ovules better protection, and nearer proximity to the sources of supply. The floral diagram is the same for the Amaryllidaceae as for the Liliaceae. (3) The Snowdrop (*Galanthus nivalis*, L.), or the Snow-flake (*Leucojum*, L.) illustrate a primitive state of this epigynous type where all the parts of perianth and androecium are separate. A more advanced type, showing not only epigyny but also cohesion of the perianth, and adhesion of the stamens to it, is seen in *Narcissus*.

(4) In the Daffodil (*N. pseudo-Narcissus*, L.), the same floral diagram (Fig. 397) and floral formula apply. But here the coherent perianth springs from the summit of the inferior ovary as a tube which separates upwards into six widely spreading segments. At the level where they diverge the tube appears to be continued into a wide trumpet-shaped *corona*. This is an

accessory formation, and only appears late, after the other parts have been formed. From the inner surface of the perianth-tube, near to its base, arise the six epiphyllous stamens. They are closely grouped round the central style, whose stigma projects beyond them. Honey-secretion is provided by three deep glands in the septa of the ovary, and it flows into the base of the tube. The size of the flower allows entry to *humble-bees*, which, passing from flower to flower, make cross-pollination probable.

Narcissus poeticus, L., the Pheasant's Eye, is a species of similar construction, but with white perianth, and a corona fringed with red. Its tube is, however, narrow, and the anthers and stigma almost fill its opening. Thus it is inaccessible to bees; but its white colour, heavy scent, and the length of the narrow tube fit it for pollination by long-tongued, night-flying *moths*. These three types of Amaryllids show how the same floral structure may be modified as a mechanism for pollination by different types of insects.

Family: IRIDACEAE. *Example:* YELLOW FLAG.

(5) Those Liliales which have inferior ovary and only three stamens, are grouped as the Iridaceae, of which the native Yellow Flag (*Iris pseudacorus*, L.)

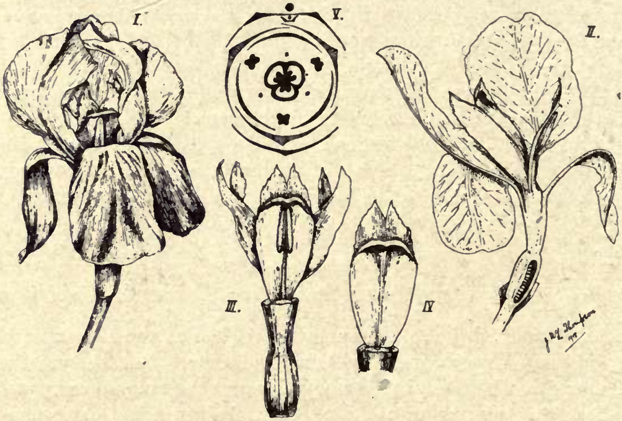


FIG. 400.
Iris pseudacorus, L. I. Complete flower. II. Same cut in median section. III. Flower with perianth removed. IV. Single lobe of petaloid style, with stigmatic lip. V. Floral diagram.

serves as an example. It has a branched and strongly rooted perennial stock (see Fig. 112, p. 164), and each branch ends in an annual foliage-shoot, with sword-shaped leaves, sheathing at the base. The apex of certain shoots extends upwards into the cylindrical flowering shoots, which bear their first flower distally; a second flower arises subsequently in the axil of a bract below it, and others may follow, in sympodial arrangement.

The large yellow flower is composed of the following parts (Fig. 400):

Perianth, segments 3 – 3, gamophyllous at the base, superior; the outer series broad and recurved, the inner narrower, and erect.

Androecium, stamens 3+0, free, epigynous, anthers opening outwards. It is the inner series that is absent.

Gynoecium, carpels 3, syncarpous, styles three petaloid ; ovary inferior, trilocular, with axile placentation ; ovules numerous, anatropous (Fig. 203, p. 255).

The *fruit* is a dry loculicidal capsule, and the flattened albuminous seeds are scattered by the wind.

Pollination. The flower of *Iris* is more specialised in relation to insect-agency than most of the Iridaceae. Many of them, such as *Ixia*, or *Sisyrinchium*, have flowers not unlike the Snowdrop, but with only three stamens. *Gladiolus* has the same, but it is slightly zygomorphic. (6) *Crocus* has a tubular perianth greatly elongated, so that while the ovary is seated just above the underground corm, the perianth, stamens, and stigmas are above ground. But *Iris* is the most specialised of them all. Its peculiar features are that the three stamens, which open outwards, are enclosed each between one of the broad outer perianth-segments and one of the three broadly petaloid styles (Fig. 400, III. IV.). The tip of each style is two-lobed, and bears a projecting lip on its lower and outer surface. This is the *stigma*. The fact that the styles are opposite the stamens, and these opposite the outer perianth-segments, shows that it is the *inner* stamens that are wanting (V.). Honey is secreted by the inner surface of the perianth-tube, and collects round the base of the styles. Each third of the flower may be pollinated independently by humble-bees, which force their way between the perianth-segment and its opposing style. On entering, if they bring pollen, it is swept off on the projecting stigmatic lip ; the stamen then deposits a fresh supply of pollen upon his body, which he carries away. Self-pollination is mechanically impossible ; but cross-pollination results with high probability from a succession of visits, either to other thirds of the same flower or to different flowers. In many forms of *Iris* the parts fit so exactly as to exclude small and weak insects that would not effect pollination, but this exclusion is less perfect in others. *Iris* may be held to show a culmination of pollination-mechanism as seen in the Liliales.

ORDER: ORCHIDALES.

Family: ORCHIDACEAE. *Example:* SPOTTED ORCHIS.

(7) The Spotted Orchis (*Orchis maculata*, L.), which flowers early, in damp grassy ground, will serve as an example of a still higher specialisation of the flower for cross-pollination by insect-agency, which characterises the Orchidaceae. The plant is perennial, and in summer is seen to consist of an upright axis bearing sheathing leaves, and a distal spike of flowers. This springs from the apex of a palmate storage-tuber of the previous year, now shrivelled ; while a second similar tuber, young and plump, is developing as storage for the next season (Fig. 401). The new tuber bursts through from the axil of one of the lowest leaves, and bears a terminal bud seated on swollen mycorhizic roots directed obliquely downwards (Fig. 151, p. 201). Normal roots also arise from the base of the shaft. By a succession of such tubers the plants perennate from year to year.

Each flower of the spike is sessile in the axil of a large leafy bract, and is of an epigynous Liliifloral type, but specialised so as to be an accurate

FIG. 401.
Whole plant of *Orchis maculata*, including the swollen mycorhizic roots. (After Figuier.)

mechanism for pollination (Fig. 402, I). The inferior ovary itself constitutes the stalk of attachment of the sessile flower. It shows ridges, the spiral turns of which indicate that the flower has been inverted by a half-circle-twist of the ovary (*resupinate*) (II. III.). The anterior side is thus turned to the front facing the bract. This is essential for the success of the *strongly zygomorphic flower* as a pollinating mechanism.

The ground-plan of the flower is shown in Fig 402, IV.; it consists of:

Perianth, segments 3 + 3, polyphyllous, superior. The three outer segments are small, and of about equal size, the odd one being anterior (1). The three inner are very unequal. The posterior segment, turned by resupination to the front, forms a large platform, or *labellum* (6), and it is dilated downwards into a long *spur* (*sp*). The two smaller, together with the outer anterior

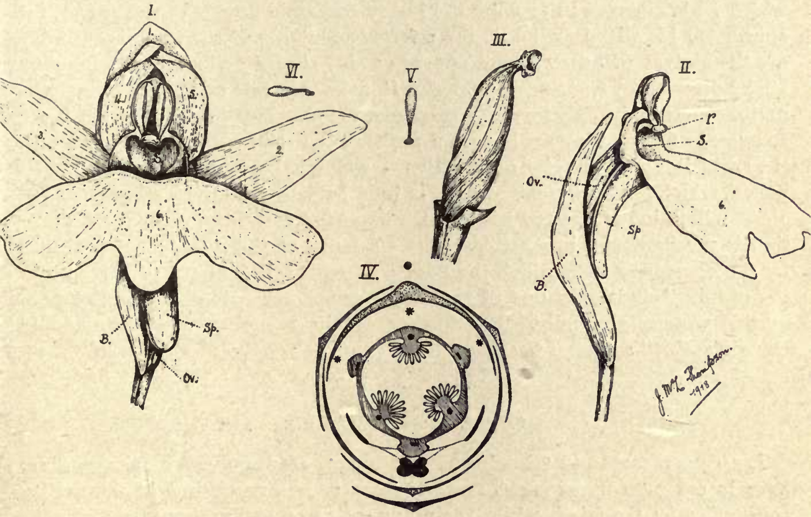


FIG. 402.

Flower of *Orchis maculata*, L. I. Whole flower in frontal view. II. Lateral aspect, perianth partly removed. III. Young fruit. IV. Floral diagram. V. VI. Pollinia in erect and curved positions. 1-6 = perianth-segments; (1) is really the anterior, but by resupination the posterior segment; 6 is the labellum, actually posterior, but by resupination the anterior segment. *B* = bract; *sp* = spur; *ov* = ovary; *s* = stigma; *r* = rostellum.

segment, form a hood-like group over the *column*, which rises just behind the open entrance to the spur. It is the result of fusion of the single stamen with the short style.

The *Androecium* is represented only by a single *anterior, fertile stamen*, which, owing to the resupination, faces the observer: each of its two purple anther-lobes shows when ripe a longitudinal slit of dehiscence. The downward directed, but really apical end of the anther is covered by the small globular *rostellum*, which obstructs the entrance to the spur (Fig. 402, I. II.).

The *Gynoecium* consists of three carpels, syncarpous and inferior. Of the three stigmas one which is not receptive is represented by the rostellum (*r*), the other two are merged into a hollow oval stigmatic surface situated below the rostellum (*s*). A transverse section of the ovary, preferably of a flower already fertilised, shows a single cavity, with three parietal placentas, and very numerous minute ovules.

The *Fruit* matures as a dry capsule, splitting by six longitudinal slits into three larger and three smaller strips, which remain united at their ends. The minute seeds are scattered by the wind.

Pollination. The flower being resupinate, the large posterior labellum projects forward as a convenient platform for the visiting insect, while the entry to the spur is presented directly to his proboscis just below the column. But the passage is obstructed by the rostellum. On inserting his proboscis this is pushed aside. As it breaks away it lays bare two sticky discs, which adhere to his proboscis, their cement setting firmly in the few seconds during which he is engaged in probing the honey-containing tissue at the base of the spur. On his withdrawing it, the coherent contents of the two anther-lobes are themselves withdrawn, and appear as *club-shaped pollinia*, fixed by their sticky discs in an erect position. But in a few seconds this position changes, and they curve strongly forwards (Fig. 402, V. VI.). Meanwhile, if he has flown to another flower, they are in such a position that as he inserts his proboscis, they will impinge directly on its stigma, which is below the rostellum. The pollen, which is in coherent masses, is then held by the sticky stigma. Thus cross-pollination is effected with a high degree of certainty, while self-pollination is mechanically impossible. The efficiency of the mechanism is shown by the constancy with which the Spotted Orchis sets its fruit as it grows in the open. This is only one of the very various methods of pollination seen in this wonderful family. For further details reference may be made to Darwin's *Fertilisation of Orchids.*

ORDER: GLUMALES.

The Cyperaceae and Gramineae, which are grouped under this heading, have in common hypogynous flowers, more or less specialised in relation to *pollination by the wind*, while their flowers are often grouped in dense inflorescences. The Juncaceae may be associated with them as a Liliifloral type only slightly modified. The construction of their flowers may be referred in origin to the Liliaceous type, but the perianth is inconspicuous, and the pentacyclic, usually trimerous structure is more or less reduced in the number of the parts. The name *Glumiflorae* refers to the fact that the bracts are usually stiff and dry, and are called *Glumes* or *Paleae*, which constitute the "chaff" of Grasses. The gynoecium is superior, and though it may be trilocular with numerous ovules in the less specialised forms, in the more advanced Sedges and Grasses it is unilocular, and contains only a single ovule. The fruit then matures as a Grain, or Nut. The plants are mostly annual or perennial herbs, frequently with long internodes. The alternate leaves are sheathing below, with a simple grass-like blade, and often a ligule projecting upwards at the junction of sheath and blade.

Family: Juncaceae. *Example:* Field Wood-Rush.

(8) The Field Wood-rush (*Luzula campestris*, Willd.) is a perennial very common on poor grass-land. It has a Grass-like habit, but its flowers are constructed on the Lily-type. The root-stock produces leaves with sheath and blade, but no ligule. The axis elongates upwards into an inflorescence

bearing numerous flowers in a compact cymose group, with chaffy bracts. The flower is constructed of:

Perianth, segments 3+3, polyphyllous, inferior, dry and chaffy.

Androecium, stamens 3+3, free hypogynous.

Gynoecium, carpels 3, syncarpous, superior, with three long feathery stigmas, united below into a short style. Ovary trilocular, with one ovule in each loculus (Fig. 403, *b*, *c*).

Fruit, a capsule dehiscent loculicidally. Seed with starchy endosperm.

FIG. 403.

Juncus lamprocarpus. *a*, Part of an inflorescence; single flower (*b*) and gynoecium (*c*) magnified. (Strasburger.)

FIG. 404.

Eriophorum augustifolium. 1, inflorescence. 2, a single spikelet. 3, single flower. 4, flower with bract removed. 5, fruit. (After Hoffmann; 1, about nat. size; the others × 3-5.) (Strasburger.)

Pollination. The flower is strongly *protogynous*; the feathery stigmas project, while the perianth is still closed over the unopened stamens. Later the stigmas wither, the perianth expands, and the anthers burst, setting free the dry dusty pollen, which is readily shaken out, and carried away by the breeze. There is no honey-secretion, or other attraction for insects, but cross pollination is almost certain by the agency of wind. Self-pollination is prevented by the marked protogyny. Nevertheless fruit is almost uniformly produced.

The chief genus is *Juncus*, to which the Rushes belong. They are mostly plants of moist habit, and of little feeding value for stock. Their presence in grass-land is an indication of the need for draining.

Family: CYPERACEAE. *Examples:* COTTON-GRASS, SEDGE.

(9) The Cotton-Grass (*Eriophorum vaginatum*, L.) is a tufted perennial herb of swampy moorlands, marked by its single cottony heads when in fruit. The flowering head rises about a foot from the root-stock, and is composed of a single spikelet of flowers in the axils of glume-like bracts. Each hermaphrodite flower is constructed as follows:

Perianth, inferior, represented by numerous bristles, which are developed relatively late, and mature into the "cotton" of the fruit.

Androecium, stamens three, hypogynous, representing those of the inner whorl.

Gynoecium, carpels three, syncarpous, and superior, with three stigmas. The ovary is unilocular, with a solitary ovule (Fig. 404).

Pollination is effected by the wind, which also carries out the transfer of the fruit.

Fruit, a trigonous nut, with the cottony tuft of the persistent perianth attached at its base. The floral structure suggests a modification of the Liliaceous type, by cottony development of the perianth, loss of the three outer stamens, and reduction of the ovary to a single loculus with one ovule.

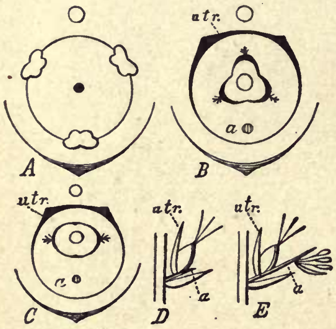


FIG. 405.

A, floral diagram of a male flower of *Carex*; *B*, of a female flower with three stigmas; *C*, of a female flower with two stigmas. *D*, diagram of female flower of *Carex*. *E*, diagram of the hermaphrodite spikelet of *Elyna*: *a*, secondary axis; *utr.* utricle or bract of secondary axis. (After Eichler.) (Strasburger.)

(10) For the structure of a Sedge, any of the following species of *Carex* will serve (*C. glauca*, Murr; *pallescens*, L.; *pendula*, Huds.; *hirta*, L.; *flava*, L.; or *binervis*, Sm.). The Sedges are perennial herbs of swampy ground, which put up long flowering shafts, each bearing several spikes of *unisexual flowers* (Fig. 405). In the species named, one or more of the distal spikes bears only *male flowers*: the lower lateral spikes bear *female flowers*. In the axil of each glume-like bract of the male spike is a male flower consisting only of three stamens, with no perianth or gynoecium. In a similar position on the female spikes there are found flask-shaped bodies (*perigynia*), through the open throat of which at flowering a three-branched stigma projects. The *perigynium is a bract enveloping the female flower*, which has no perianth, and no androecium, but consists of three, or sometimes two carpels, syncarpous and superior. The ovary is unilocular, the ovule solitary, and fruit a nut. Here the flower is still more simple than in the Cotton-Grass, for there is no perianth, and as the flowers are unisexual, all that remains are the three stamens in the male, and the three carpels in the

female. *Pollination* is by the wind. A large number of flowers of simple structure are aggregated in the inflorescence: cross-pollination is therefore probable.

The Sedges are of little value for fodder. Drainage of the wet ground in which they grow promotes the more valuable Grasses, from which they are distinguished by their solid stems and leaf-divergence of $\frac{1}{3}$, while in Grasses it is $\frac{1}{2}$: also by the median position of the embryo in the seed, while in Grasses it is placed laterally.

Family: GRAMINEAE. *Example:* COMMON RYE-GRASS.

(11) The Rye-Grass (*Lolium perenne*, L.) is a common grass of meadows and road-sides; its variety *italicum* is often cultivated for fodder. It has leafy stolons and ascending flowering shoots, and it is easily recognised

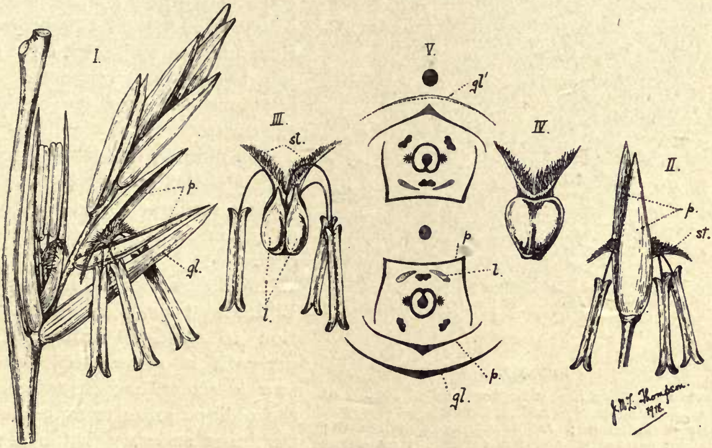


FIG. 406.

Inflorescence and flower of *Lolium perenne*. I. shows part of the main rachis, with one lateral spikelet in the axil of the single glume (*gl*). II. a single flower with its two paleae (*p*), pendent stamens, and feathery stigmas (*st*). III. flower dissected out, showing lodicules (*l*). IV. the gynoecium. V. floral diagram: *gl* = glume; *gl'* = glume which is wanting in *Lolium*; *p* = paleae; *l* = lodicules.

amongst common Grasses by their long flattened form. Its flowers open in succession, so that it can be obtained in the flowering state throughout the summer. The flowers can be made to open at any time by keeping them warm, and in water.

The inflorescence is borne on a long stalk, above the uppermost foliage leaf, which has a split sheath, ligule, and lamina. It is a compact, compound spike, composed of *spikelets* placed edgewise, alternately on its two sides, with one terminal. Each lateral spikelet, which consists of an axis bearing flowers alternately in two rows, arises in the axil of a bract, or *outer glume* (Fig. 406, I.). In most Grasses there is a second, or *inner glume*, on the side opposite to the outer; but this, being unnecessary for protection in the dense inflorescence of the Rye-Grass, is not present, except in the terminal spikelet. Each flower is ensheathed in two further bracts or *paleae*: the *lower* and outer is *anterior*, the *upper* and inner is *posterior*, and the flower itself lies between them. At flowering they gape widely apart, so as to expose the parts of the flower. If a flower be found in this condition, or if the lower palea be forced back, the flower, as seen from the anterior side, will show the following parts:

(i) Two *lodicules*, which are minute, colourless, hypogynous scales, right and left of the median plane. It is by their swelling that the paleae are forced apart at the time of flowering.

(ii) Three *stamens*, hypogynous, free, with long flexible filaments, and versatile anthers, bearing powdery pollen. One stamen is median and anterior, the two others obliquely posterior.

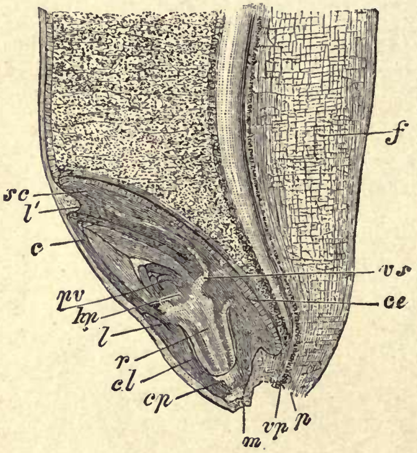


FIG. 407.

Part of a median longitudinal section of a grain of Wheat, showing embryo and scutellum (*sc*). *vs* = vasc. bundle of scutellum; *ce* = its columnar epithelium; *l'* = ligule; *c* = sheathing part of cotyledon; *pv* = vegetative cone of stem; *hp* = hypocotyl; *l* = epiblast; *r* = radicle; *cl* = root sheath; *m* = micropyle; *f* = funiculus; *vp* = vascular bundle of funiculus; *f* = lateral wall of groove; *cp* = pericarp. (× 14.) (After Strasburger.)

(iii) Certainly the *gynoecium* consists of a pear-shaped superior ovary, grooved on the posterior side, and bears distally, right and left, two feathery stigmas. Dissection shows a single ovule in the ovary.

The number of such flowers in each spikelet varies: 8 to 10 are common numbers, and they open at intervals in acropetal succession.

The flower may be held to be of Liliifloral type, reduced in relation to wind-pollination. The perianth is represented by the two lodicules, corresponding to the oblique anterior segments of the inner series, which being of use in separating the paleae at flowering have survived. The stamens correspond in position to the outer whorl of the Liliiflorae, while the gynoecium is held to consist of a single carpel, corresponding to the anterior carpel of the Liliiflorae. This floral structure is very constant in the Grasses, but the flowers are variously disposed in their inflorescences. The Rye-Grass may be taken as a good example for the Family, and it is easily recognised.

The inconspicuous flowers, versatile anthers, dry dusty pollen, and expanded feathery stigmas clearly indicate *wind-pollination*. Most Grass-flowers are homogamous, that is, stamens and stigmas mature simultaneously, but some are protogynous (*Alopecurus*).

The *fruit* is a dry nut, containing one albuminous seed and a *lateral embryo*. Its structure is well illustrated by the grain of wheat or maize (Fig. 407).

DICOTYLEDONEAE.

These Plants are characterised by the embryo bearing two cotyledons. The leaves are net-veined, usually with a narrow base, and a definite petiole. The stem and root show secondary thickening by means of a cambium. The flowers are usually pentamerous, or tetramerous, with distinct calyx and corolla. The plants are perennial or annual, many of the former developing as shrubs or trees.

The Dicotyledons are divided into two large series, according to the separateness or coherence of their petals. This distinction does not serve a like purpose in the classification of the Monocotyledons; it has already been seen that the very natural Family of the Liliaceae is variable in this respect (p. 495). But in the Dicotyledons the same variability within natural families is exceptional: therefore this distinction serves to give a natural separation of them into Polypetals, or *Choripetalae*, with the petals all separate from one another; and the Gamopetals, or *Sympetalae*, where there is a coherence of the petals to form a united, usually tubular corolla.

The former is undoubtedly the more primitive state. It repeats the condition usual in the vegetative region, and it is characteristic of those less specialised flowers which on many other grounds are held as less advanced. The gamopetalous state is characteristic of flowers which are more specialised as pollinating machines, and they may therefore be held as more advanced. But there is no reason to hold all plants showing gamopetaly as necessarily related to one another: this would involve the assumption that this advance had happened only once in the course of Evolution. It seems probable that in a plurality of evolutionary lines the advance was made to gamopetaly, and the student should be prepared to recognise this in any sequence in which comparison makes it appear probable. In accordance with the views thus briefly sketched the Polypetals, or *Dicotyledoneae—Choripetalae*, will be taken first.

DICOTYLEDONEAE—CHORIPETALAE.

ORDER: SALICALES.

Family: Salicaceae. *Example:* The Goat Willow.

(12) The numerous native species of Willow are trees, or shrubs, or dwarf undershrubs, which live in damp situations; almost any of them would serve to

illustrate their very simple floral structure. In the large shrubby Goat-Willow (*Salix caprea*, L.) the flowers appear grouped to form the well-known Catkins, or "Palms." These are of two sorts, distributed on different plants (*dioecious*)

Fig. 408.
Catkins of the Willow. *a*, male; *b*, female. (After Figuier.)

(Fig. 408). The *male catkins* appear bright yellow when in bloom, from their projecting stamens; the *female catkins* are more slender, and of olive-green colour. In each case the catkin is a spike. Its main axis bears darkly-coloured bracts, and in the axil of each of these is a single very simply-constructed flower.

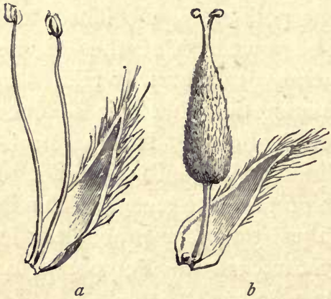


Fig. 409.
Flowers of Willow (*Salix alba*). *a*, male; *b*, female: in each case the subtending bract is also shown. (After Figuier.)

The *male flower* (Fig. 409, *a*) consists of two stamens, each with a long filament, which bears the anther, with sticky, not dusty pollen. There is no perianth, nor gynoecium; but on the side next the stem is a nectary, which secretes honey freely at flowering (Fig. 410, *A*, *d*). Other species may have three, four, or more stamens, but no other floral parts (Fig. 410, *C*). The *female flower* (Fig. 409, *b*) is also axillary. It consists only of a gynoecium of two carpels joined by their margins to form a unilocular, superior ovary with two-lobed stigma. The ovules are numerous, and the placentation parietal. A honey-gland is present here also between the flower and the main axis (Fig. 411, *A*).

Pollination. The flowers of both catkins are visited freely by insects, both bees and moths, for honey or for pollen. Self-pollination is obviously impossible, for the plants are dioecious; but crossing follows as a natural consequence of the conveyance of the sticky pollen to the protogynous female catkins by insect-visitors.

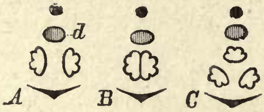


FIG. 410.
Floral diagrams of male flowers of Willow. *A* = *S. caprea*. *B* = *S. purpurea*. *C* = *S. pentandra*. (After Eichler.)

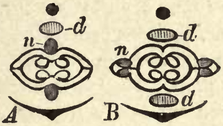


FIG. 411.
Floral diagrams of female flowers of *Salix*. *A* = *S. caprea*. *B* = *S. alba*. (After Eichler.)

The *fruit* is a tough capsule, which splits longitudinally, exposing the seeds, each with a tuft of silky hairs attached to its base, by which it is transferred by the wind.

ORDER: CURVEMBRYEAE.

Family: CARYOPHYLLACEAE. *Examples:* RAGGED ROBIN, RED CAMPION.

(13) The Ragged Robin (*Lychnis flos-cuculi*, L.) is a herb of damp grassy ground, with perennial root-stock from which arise upright stems with simple leaves in alternate pairs. The inflorescence is a definite, regular dichasial

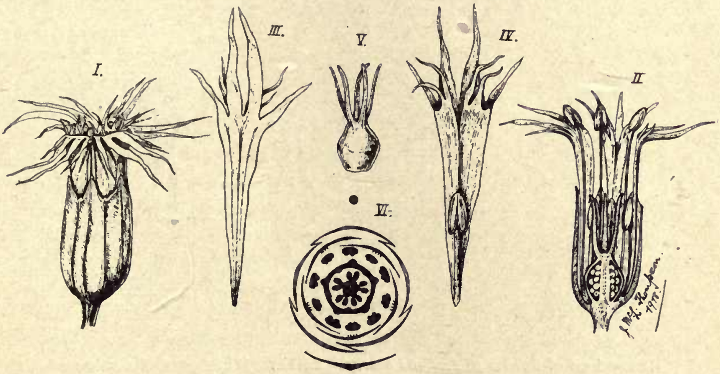


FIG. 412.
The Ragged Robin (*Lychnis flos-cuculi*, L.). I. whole flower. II. same in section. III. petal with ligule. IV. petal with ligule and petaline (inner) stamen. V. gynoecium. VI. floral diagram.

cyme: that is, the main axis ends in the first flower; branches arising in the axils of the last leaves again terminate each in a flower, and so on (compare Fig. 170, p. 224). The flower is of a radial type, with peculiar tattered pink petals, which gives the name (Fig. 412). Its constitution is as follows:

Calyx, sepals 5, gamosepalous, inferior, dilated below, and serving as a mechanical support to the weaker parts within.

Corolla, petals 5, polypetalous, inferior, deeply notched, and again divided, bearing paired ligules at the sharp angle of the claw of each.

Androecium, stamens 10, free, hypogynous, of varying length during flowering. The 5 outer opposite the sepals, the 5 inner opposite the petals.

Gynoecium, carpels 5, syncarpous, superior; ovary unilocular, ovules numerous, on free central placenta. Styles and stigmas 5, rising separately from the apex of the ovary.

Pollination. Nectar is secreted at the base of the stamens, and the flowers are visited by many insects, especially butterflies and moths. The flowers

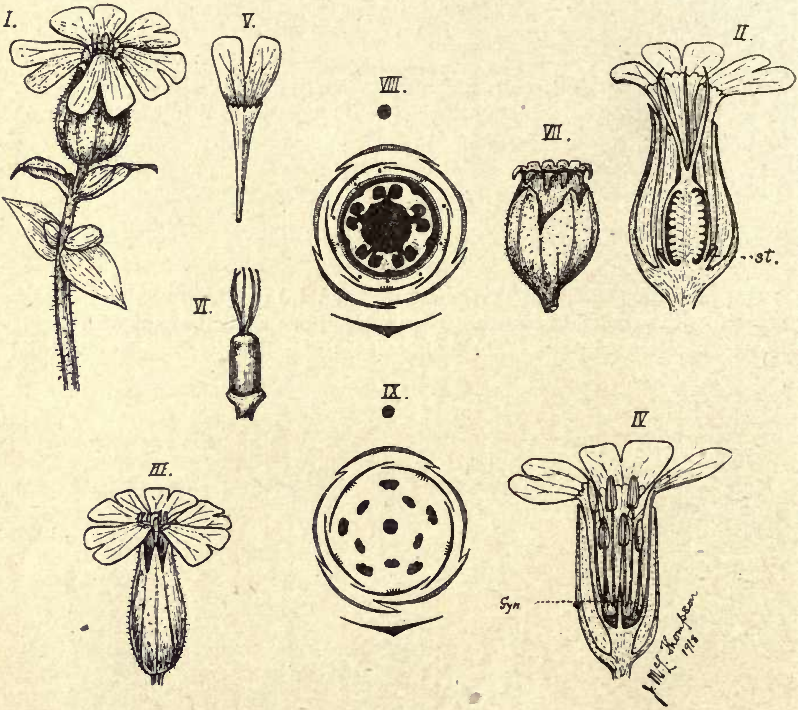


FIG. 413.

Dissections of flowers of *Lychnis diurna.* I., II., VIII., the pistillate flower in which the stamens are represented only by staminodes (*st*). III., IV., IX., the pistillate flowers in which the gynoecium is represented only by a vestigium (*gyn*).

are *protandrous*; in the first stage the 5 outer stamens shed their pollen at the entrance of the tube; later the 5 inner stamens do the same; finally the 5 stigmas grow up and fill the entrance to the flower. An insect visiting the flower in either of the first stages will remove pollen on its proboscis, which it may deposit on another flower in the third stage. Intercrossing is thus probable, though self-pollination is possible.

(14) In the Red Campion (*Lychnis diurna*, L.), two types of plant are found: some with thinner stems and smaller leaves bear only staminate flowers, others with more robust habit bear pistillate flowers. These should be examined and compared (Fig. 413). In the staminate flowers the Calyx and Corolla are

essentially as above described. Also the 10 stamens, but they are of unequal lengths, and they surround a minute green central process, which represents the *abortive gynoecium*. The pistillate flowers are of like structure; but here the androecium is represented by ten small conical *staminodes*, while the gynoecium is fully developed, with five carpels, a large ovary with five styles and stigmas, and numerous ovules on a free central placenta.

Pollination. Comparing the two species: in both, nectar is secreted at the base of the tube, and protected by hairs, while the weak petals and stamens are supported by the firm gamosepalous calyx. In the Ragged Robin there is a separation of the sexes in time, it being markedly *protandrous*, which gives a probability of intercrossing as a consequence of repeated insect-visits. In the Red Campion the sexes are separated in space, being borne on distinct plants. This renders self-pollination impossible, and cross-pollination obligatory. That the latter is the derivative state is clearly shown by the presence of the abortive stamens, and pistils.

The *fruit* is a dry capsule, which opens by teeth at the distal end, and the numerous curved, albuminous seeds are scattered as it is shaken in the wind.

The products of the Order are unimportant. It is related to the Goosefoot Family (Chenopodiaceae).

ORDER: POLYCARPICAE.

Family: RANUNCULACEAE. *Examples*: MARSH-MARIGOLD, BUTTERCUP, MONKSHOOD.

The Buttercup Family is relatively primitive, as indicated by the variability of its floral construction, by the number of its parts, and the character and composition of the perianth: also by the fact that all the parts are inserted separately upon a conical receptacle. It includes herbs or shrubs of temperate and cold climates, with alternate ex-stipulate leaves, having palmate venation. They are mostly acrid, and poisonous.

(15) A simple type of their floral construction is seen in the Marsh-Marigold (*Caltha palustris*, L.), common in wet places. It is a coarse herb, with creeping rootstocks and cordate radical leaves. The flowering stems are sub-erect, with a few leafy bracts and cymose branching. The large yellow flowers consist of:

Perianth, a single series of *petaloid sepals*, 5 or more, imbricate in bud: the outermost obliquely anterior; polyphyllous, and inferior.

Androecium, stamens indefinite (80 to 150), free, hypogynous, dehiscent by lateral slits.

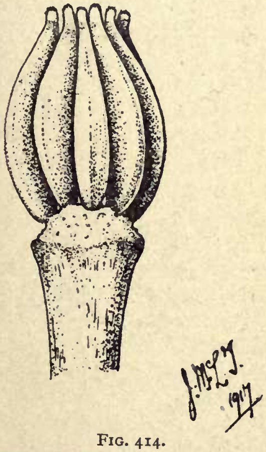


FIG. 414.
Pistil of *Caltha*, with numerous apocarpous carpels. Enlarged.

Gynoecium, carpels 5 to 10, apocarpous, superior. They are follicles, with margins turned centrally, to which the numerous ovules are attached in two rows (Fig. 414). Each has a terminal stigma, while near the base of each, on either side, is a group of honey-secreting hairs. Ovule anatropous.

The *pollination* is not highly specialised; the symmetry is radial; the attractions are colour, and honey on the carpels; there is slight protandry, and the stamens mature in succession, so that the supply of pollen is prolonged. There is a probability of intercrossing. but self-pollination is possible.

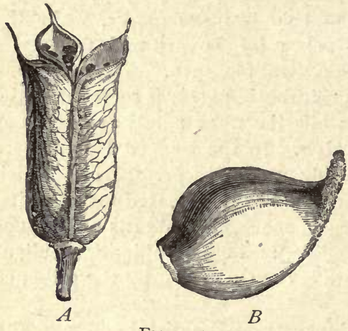


Fig. 415.
A, Follicles of Aconite. (After Figuier.).
B, Achene or nut of Buttercup. (After Figuier.)

The *fruit* is a group of follicles, which open by their ventral sutures, and gaping widely upwards allow their seeds to escape (Fig. 415, *A*).

(16) The Buttercup (*Ranunculus acris*, L., or other species) is more specialised, having both calyx and corolla; but the flower is constructed on a similar plan; as follows: (Fig. 416.)

Calyx, sepals 5, polysepalous, inferior, imbricate in bud, the outermost being obliquely anterior.

Corolla, petals 5, polypetalous, alternating with the sepals, inferior yellow, with a honey-pouch on the upper face of each, near the base (Fig. 416, 2).

Androecium, stamens indefinite, free, hypogynous; the outermost maturing earliest.

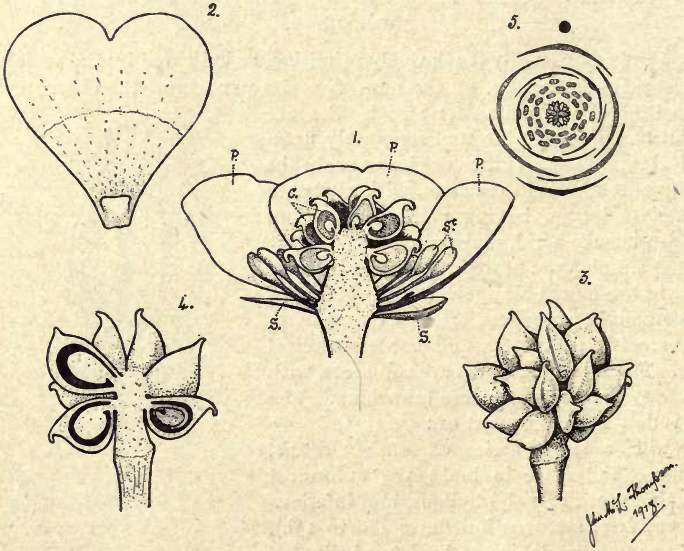


Fig. 416.
Buttercup (*Ranunculus acris*, L.). 1, Flower in median section. 2, a single petal. 3, the gynoecium. 4, the same in section. 5, floral diagram.

Gynoecium, carpels indefinite, apocarpous, superior: each contains only a single anatropous ovule; otherwise similar in form to the fewer and larger carpels of *Caltha*.

The general conditions of *pollination* are the same as in *Caltha,* but with honey at the base of the coloured petals.

Each carpel matures as a dry indehiscent *nut,* falling away with its single seed within (Fig. 415, *B*). Comparing with *Caltha* the flower is more elaborate and probably derived from the type of the Helleboreae, by conversion of the outermost stamens, first into honey-leaves as in *Helleborus* or the Globe-Flower, then into large honey-bearing petals, as in the Buttercup (compare Fig. 180, p. 230). The carpels meanwhile had their ovules reduced to one each, while the propagative power was made up by increase in the number of carpels.

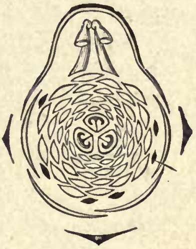


FIG. 417.
Floral diagram of *Aconitum.* (After Eichler.)

(17) The Monkshood (*Aconitum napellus,* L.) is a perennial with swollen storage roots, commonly grown in gardens: it is an important drug. Its inflorescence is a raceme, developing as a cymose panicle below. The flower shows median zygomorphy (Fig. 417), and consists of:

Calyx, sepals 5, polysepalous, inferior, corresponding in number and position to the Buttercup, but petaloid; the posterior sepal enlarged as a hood.

Corolla, petals usually 8, of which the two obliquely posterior are elongated into stalked glandular spurs (nectaries), covered by the hooded sepal; the rest are small; polypetalous, inferior.

Androecium, stamens indefinite, spirally arranged, free, hypogynous.

Gynoecium, carpels usually 3, apocarpous, superior. Follicles and their dehiscence as in *Caltha.*

Comparing this flower with *Ranunculus* or *Helleborus,* it is clearly a zygomorphic development of the same type. The flower is protandrous. The sepals give colour-attraction, and the honey is conveniently placed for humble-bees in the posterior, spurred petals, while the whole is sheltered by the hood. The protandry makes cross-pollination highly probable from successive visits. After shedding their pollen the filaments curve back so as to expose the receptive stigmas. Self-pollination is thus improbable.

ORDER: RHOEADALES.

Family: PAPAVERACEAE. *Example:* THE RED POPPY.

(18) The Common Corn Field Poppy (*Papaver rhaeas,* L.) is an annual which ripens its seeds before the corn is cut, and it is thus ready to spring again in the next season. The plant, which is bristly and contains a milky juice, consists of a leafy stem branched below. The solitary flowers are terminal on their long hispid stalks, the buds hanging down, but the stalks straighten before flowering, and in fruit (Fig. 418). The flower consists of:

Calyx, sepals 2, polysepalous, inferior, antero-posterior, falling off at the opening of the bud.

Corolla, petals 4, polypetalous, inferior, wrinkled in bud, two lateral, two antero-posterior.

Androecium, stamens indefinite, free, hypogynous.

Gynoecium, carpels 8-12, syncarpous, superior; the stigma sessile, star-shaped; the rays of the star indicate the number of the carpels. The ovary is unilocular: beneath each ray of the stigma (that is, at the junction of the carpels that compose it) a flat partition extends radially towards the centre, but without reaching it. In others of the Poppy family the carpels may be fewer, and in *Chelidonium* only two, as in the Cruciferae. The small and numerous ovules are borne superficially on these plates. *Fruit*, a dry capsule opening by pores below the stigma. Seeds with oily endosperm: they are scattered out by wind shaking the pore-capsule (see Fig. 231, p. 289).

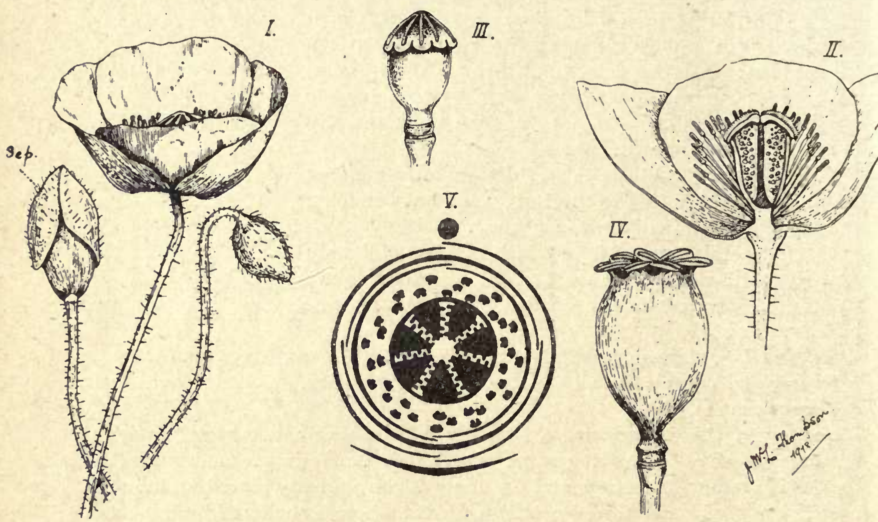


FIG. 418.

Red Poppy (*Papaver rhaeas*, L.) I. flower and buds, with sepals falling away. II. flower in median section. III. gynoecium. IV. ripe fruit, with dehiscent pores below the star-shaped stigma. V. floral diagram.

Pollination. The showy flower attracts insects, which come to collect pollen. There is no honey, and the flower is radial: it is not a highly specialised type. Promiscuous cross-pollination may follow from insect visits, but self-pollination is also possible. *Papaver somniferum*, L., the Opium Poppy, belongs to the family.

Family: CRUCIFERAE. *Example:* THE CHARLOCK.

(19) The Charlock, or Field Mustard (*Brassica sinapis*, Visiani), is the common weed that colours cornfields yellow in early summer. It is an annual, with stem and leaves bristly with stiff hairs. Its germination is shown in Fig. 3, p. 10. Its inflorescence is a raceme, but with the bracts abortive (Fig. 219). The flower, which is of radial symmetry, consists of:

Calyx, sepals 4, polysepalous, inferior; in two pairs, the outermost being antero-posterior, the inner lateral.

Corolla, petals 4, polypetalous, inferior, with a long basal claw. They are cruciform, and alternate with the sepals.

Androecium, stamens 6, free, hypogynous: two are short and lateral, opposite the outer sepals; four are longer in two pairs, opposite the inner sepals.

Gynoecium, carpels 2, syncarpous, superior; ovary bilocular, with many ovules; an ill-defined style, and a stigma with antero-posterior lobes. The ovules are curved, and seeds ex-albuminous (Fig. 3, i. ii.). *Fruit*, a "siliqua" which is a dry capsule, the lateral carpellary walls of which split from the base upwards, leaving the two placentas as a frame with the transparent septum stretched between them (Fig. 93). The septum is called "false"

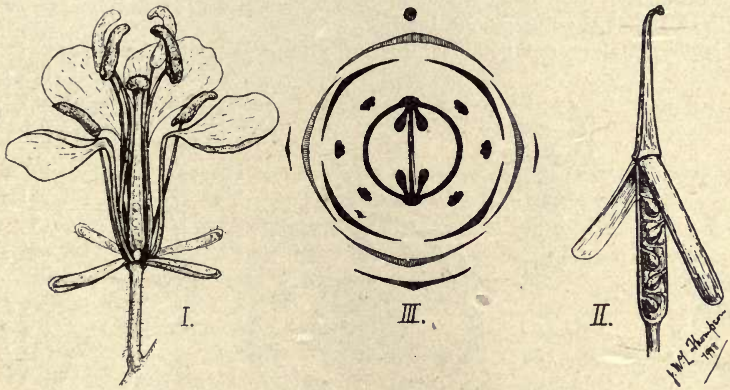


FIG. 419.
Charlock (*Brassica sinapis*, Visiani). I. flower, with parts slightly displaced. II. ripe and dehiscent fruit. III. floral diagram.

because it is formed late, by ingrowths from the two opposite placentas, the ovary being originally unilocular, as it is in the Poppies and in the Capers.

Pollination. The flowers being grouped are conspicuous, and are visited for their pollen, and for honey. The honey-secretion is by glands at the insertion of the short lateral stamens. Insects passing from flower to flower and inserting their proboscis, will probably effect intercrossing; but self-pollination is possible, and it is even provided for by the longer stamens coming in contact with the stigma as the style elongates. It is not a highly specialised type of flower and it is very constant in the Cruciferae, and may be equally well studied in the Wallflower. The structure is probably di-merous throughout, but with a fission of the median petals to form divergent pairs, and of the median inner stamens to form the four longer. This is expressed in the floral formula :—S. $2 + 2$, P $2_2 \times$, A. $2 + 2_2$, G. $\underline{(2)}$.

The construction of the flower would then be theoretically as follows:

Two antero-posterior sepals.

Two lateral sepals.

Two antero-posterior petals (by fission resulting in the four oblique petals).

Two lateral stamens, short.

Two antero-posterior stamens (by fission resulting in the four long stamens).
Two lateral carpels.

Comparison with the Poppies and the Caper Family shows this to be the probable interpretation of the Cruciferous Flower, and that it is thus referable to a dimerous origin, with regularly alternating whorls.

ORDER: GERANIALES.

Family : GERANICEAE. *Example :* THE FIELD GERANIUM.

(21) The Field Geranium (*Geranium pratense*, L.) is a strong-growing herb with opposite, palmate, and stipulate leaves. The inflorescences are lax cymose panicles (Fig. 420). Each flower consists of :

Calyx, sepals 5, polysepalous, inferior.

Corolla, petals 5, polypetalous, inferior, alternating with the sepals.

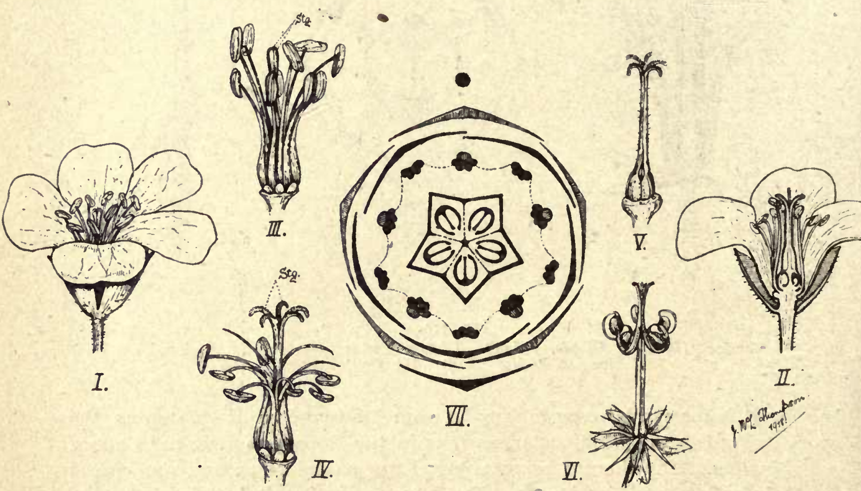


FIG. 420.

Geranium pratense, L. I. whole flower. II. the same in section. III. the stamens at time of dehiscence, the stigmas (*stg*) still closely appressed. IV. later stage with stigmas (*stg*) recurved. V. gynoecium at same stage as IV. VI. ripe fruit dehisced. VII. floral diagram.

Androecium, stamens 10, free, perigynous, with filaments widened at the base. The five petaline stamens are external, the five sepaline are internal, a condition described as "obdiplostemonous," and notable as an apparent departure from the rule of alternation of successive whorls.

Gynoecium, carpels 5, syncarpous, superior, with single style bearing five distinct stigmas. Ovary with five loculi, each containing two ovules, of which only one usually matures.

The dry *fruit* is characteristic. The style remains as a firm woody beak. At ripeness each carpel suddenly splits away longitudinally from the beak, and curving sharply, hurls out its seed to a distance (Fig. 230, p. 288).

The floral formula is S. 5, P. 5, And. 5 + 5, G. 5.

Pollination. The flower is showy, and attracts also by honey secretion outside the bases of the stamens. It is markedly protandrous. The five outer stamens open first, followed by the five inner, but the stigmas remain closely appressed together (III.), and expand only after the pollen is shed, when the anthers curve away from them (IV.). This separation of the sexes both in time and space makes self-pollination highly improbable, and the plant depends upon cross-pollination resulting from insect visits. In other species of *Geranium*, especially the smaller-flowered, self-pollination occurs, the separation of the sexes being less marked. On the other hand in the Scarlet Geranium of gardens (*Pelargonium*), the flowers are slightly zygomorphic, and there is a deep honey-gland sunk in the pedicel opposite to the posterior sepal, a specialisation still more perfected in the Nasturtium (*Tropaeolum*).

ORDER: TRICOCCAE.

Family: EUPHORBIACEAE. *Example:* THE CAPER-SPURGE, OR OTHER SPECIES.

The Euphorbiaceae, or Spurges, are a very large Family, of which the genus *Euphorbia* is an extreme type. They have reduced, unisexual flowers, which are sometimes isolated, with their floral envelopes developed, as in *Phyllanthus*; but in *Euphorbia* and others the flowers are closely grouped together, so that a whole inflorescence may appear, and even functionate as a single flower. The less reduced types indicate that their relation is with the Gruinales, from which they may be regarded as an interesting reduction-series.

(23) *Euphorbia* is represented in the British Flora by many species. They are herbs or small shrubs with smooth surface, and milky juice. Their leaves are exstipulate, but that is not general for the Order. The inflorescence is very complicated, the apparent unit being the flower-like *cyathium*, which is itself a very compact, compound spike (Fig. 421, I. II.). These units are borne like flowers on an inflorescence, which is usually a cymose umbel. The cyathium itself consists of an external cup, which looks like a calyx, but is really formed of five coalescent *bracts*, forming an *involucre*. On its margin four, or occasionally five, yellowish *glands* are borne, a blank space being left on one side; there two teeth of the bracts are found, where the missing gland might be. Within the cyathium a single stalked *female flower* occupies the centre: it projects from the cup, and hangs over the side between the two bracts which are not separated by a gland. It consists of a gynoecium of three syncarpous carpels, having three styles with bifid stigmas. It is trilocular, and one pendulous, anatropous ovule lies in each: the upward-directed micropyle is covered by a fleshy outgrowth known as the caruncle, which is characteristic. At the base of the ovary is a distended ring, held to represent the abortive perianth. The gynoecium is thus superior.

Around the female flower are a number of structures which look like stamens: they are associated with minute hairy bracts. Each of these is a *male flower* (VI.), consisting of a single stamen with a bilobed anther. The stalk which looks like a filament bears about half way down a constricted joint, which is believed to mark the place of an abortive perianth. The part below it would then be pedicel, above it the filament. In *Anthostema* the perianth is better developed

(Fig. 169, iii. p. 222). If these conclusions be correct, then the Cyathium is properly regarded as a condensed inflorescence.

The *fruit* is a capsule ; when it is ripe the carpels separate elastically from a central column. This type of carpel, though in larger number, is seen in *Hura* (Fig. 94, p. 134), another member of the Family. This type of carpel is known as a coccus, hence the name Tricoccae, for the number is usually three. The similarity to the fruit of the Geraniaceae is striking.

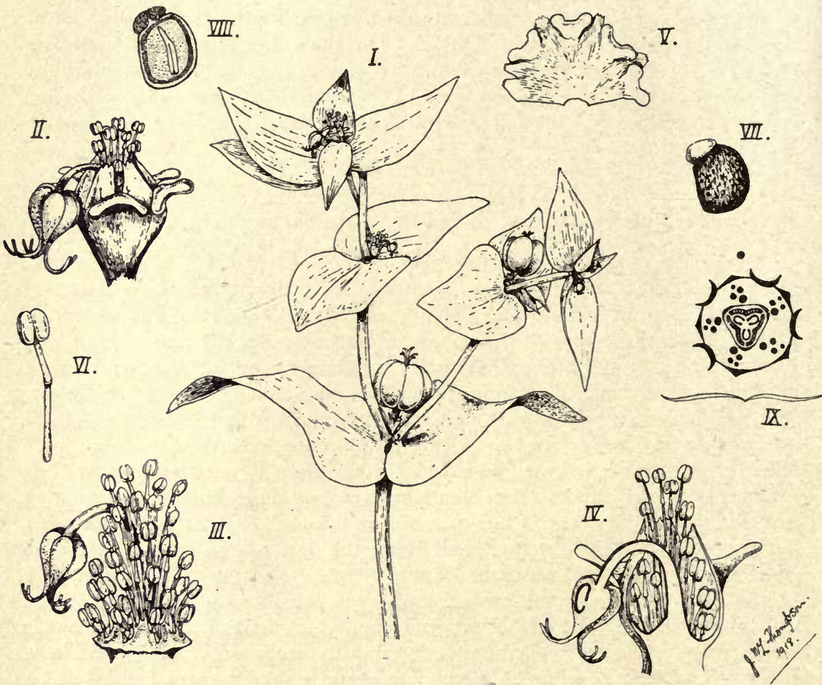


FIG. 421.

Euphorbia Lathyris, L. I. flowering shoot. II. a single cyathium. III. Cyathium with involucre removed. IV. same in section. V. the involucre. VI. a single male flower. VII. ripe seed with caruncle. VIII. same in section. IX. diagram of a cyathium.

Pollination. The stigmas in any Cyathium have as a rule ceased to be receptive before the pollen of the same cyathium is shed. Thus the inflorescences are *protogynous*.

ORDER: SAXIFRAGALES.

The Saxifragales probably represent a type from which a number of derivative groups have sprung. A general floral formula for them is S. n, P. n, And. $n+n$, G. n, with the ovary superior, and in the simplest examples, such as *Astilbe*, the carpels are separate and many-seeded pods. This type may be varied by increase in number of the stamens, or of the carpels ; by the sinking of the carpels more or less completely into the receptacle, so as to give a half-inferior or an inferior ovary ; and in some cases by reduction of the number of the carpels to two or only one. The number of ovules may also be reduced. But still the main framework of the flower remains the same. Most of the related plants bear stipulate leaves.

Family : SAXIFRAGACEAE. *Example :* MEADOW SAXIFRAGE.

(24) The White Meadow Saxifrage (*Saxifraga granulata*, L.) is a frequent herb of grass-land, and banks. It bears at its base pink bulbils, by which it multiplies vegetatively, associated with radical leaves. The flowering stem bears leaves below, and a definite cymose inflorescence above, with few large flowers. The whole plant has glandular hairs. The flower-stalk widens out into a green hemispherical region : this encloses the base of the ovary, which is thus half-inferior ; while the other floral parts are inserted on its margin (Fig. 422). The flower consists of :

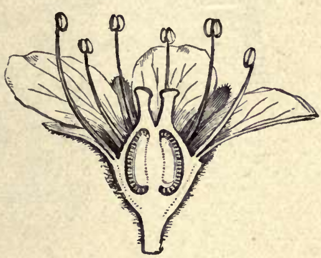


FIG. 422.

Median section of the flower of Saxifrage, showing the carpels half sunk in the receptacle, and coherent for the greater part of their length. (After Figuier.)

Calyx, sepals 5, polysepalous, seated on the margin of the receptacle ; the odd sepal is posterior.

Corolla, petals 5, polypetalous, alternating with the sepals.

Androecium, stamens 5 + 5, the petaline outermost (obdiplostemonous) inserted round the half-sunk carpels, *i.e.* half-epigynous.

Gynoecium, carpels 2, half-inferior, oblique ; united in their lower part, but separate above, with distinct styles and capitate stigmas (half-syncarpous). Ovary bilocular, ovules numerous, placentation axile.

Fruit, a dry capsule, with longitudinal dehiscence.

Pollination. The flowers are protandrous, the inner series of stamens ripening first ; then the outer. Nectar is secreted at the upper surface of the ovary. The flowers are visited by flies and small bees, and repeated visits will give a high probability of cross-pollination. But the flower is not highly specialised, and self-pollination is possible.

The London Pride (*Saxifraga umbrosa*, L.) will serve as an alternative example, though the flowers are smaller and more numerous, and the carpels are not so deeply sunk. It is pollinated by small flies.

(25) The Red-Flowering Currant (*Ribes sanguineum*, Pursh) is native in North America, and is commonly grown in gardens. It serves as an example of the Ribesiaceæ, which are usually grouped with the Saxifragaceæ, notwithstanding their inferior ovary, and five stamens. The Gooseberry or Currant of gardens would serve equally well.

The Inflorescence is a pendulous raceme (Fig. 423), arising in the axil of a foliage leaf of the previous season. The flowers are hermaphrodite and actinomorphic, composed as follows :

Calyx, sepals 5, polysepalous, superior, crimson ; odd sepal posterior.

Corolla, petals 5, polypetalous, alternating with sepals, paler coloured.

Androecium, stamens 5, alternating with petals; seated on rim of receptacular tube.

FIG. 423.
Inflorescence of Currant: a raceme. (After Figuier.)

FIG. 424.
Berries of the Currant. (After Figuier.)

Gynoecium, carpels 2, syncarpous, ovary inferior, unilocular, with numerous ovules seated on lateral placentas, ovules anatropous.

Fruit, an inferior berry (Fig. 424).

Pollination. The flowers are attractive by colour, and by grouping in racemes. Honey is secreted at the base of the receptacular tube. The flowers are very slightly protogynous, and are pollinated chiefly by bees; but self-pollination is also possible.

ORDER: ROSALES.

Family: ROSACEAE. *Examples:* STRAWBERRY, APPLE, CHERRY, ETC.

The Rosaceae are herbs, shrubs, and trees, with alternate stipulate leaves. They are widely distributed, especially in temperate zones, and are largely represented among cultivated flowers and fruits. The flowers are actinomorphic, and usually pentamerous; but the stamens are often numerous. The Family is specially instructive from the variability in development of the receptacle, so that it includes perigynous and epigynous types. There is also great variability in the number of the carpels. But still it is a very natural group, the flowers being referable to the same fundamental construction as the Saxifragaceae, to which they are closely allied.

Family: ROSACEAE. *Examples:* APPLE, STRAWBERRY, ROSE, CHERRY.

(26) The Apple (*Pyrus malus*, L.) is a small tree with long vegetative shoots and short spurs, upon which the flowers are borne. The leaves are stipulate. The flowers appear in groups, one terminal on the spur, the rest in the axils of the bracts below it. Each flower, together with two bracteoles, is borne on an elongated stalk, which swells immediately below the calyx into the enlarged *inferior ovary*. It is thus *epigynous* (Fig. 425), and consists of:

Calyx, sepals 5, polysepalous, superior; the odd sepal is posterior.

Corolla, petals 5, polypetalous, superior, alternating with the sepals.

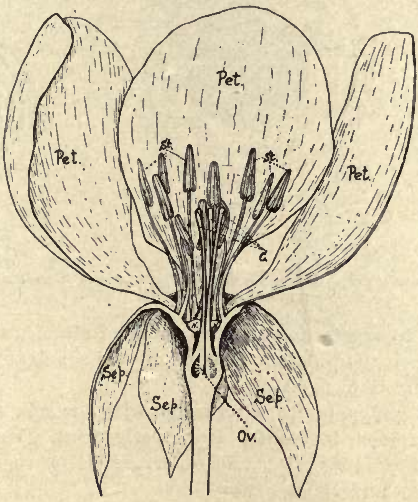


FIG. 425.

Vertical section through a flower of the Quince (*Cydonia*). *sep* = sepals. *pet* = petals. *st* = stamens. *c* = apices of the carpels, elongated into styles. *ov* = ovules. *n* = nectaries. The receptacle is here hollowed out, so that the carpels appear sunk down into a cavity. (After Church.)

Androecium, stamens indefinite, free, epigynous.

Gynoecium, carpels 5, syncarpous, inferior; five distinct stigmas are borne on styles separate above, but more or less distinct below. Ovary with five loculi, and several ovules in each (Fig. 426, *A*).

Fruit, consists of the inferior ovary crowned by the persistent calyx. The five carpels are sunk in the succulent tissue of the receptacle, from which they are not distinctly marked off. Their inner cartilaginous wall forms the "core," and one or more "pips," or seeds, are contained in each.

Pollination. The flowers are attractive by colour and easily accessible honey secreted on the concave surface within the stamens. They are slightly protogynous, but are not highly specialised. Insects collecting honey and pollen will carry out cross-pollination, but self-pollination is also possible.

(27) The Wild Strawberry (*Fragaria vesca*, L.) is a perennial herb with ternate, stipulate leaves, borne upon a sympodial rhizome. The apex of the

leafy shoot of the preceding year grows up into the inflorescence of the current year, while it is upon a lateral bud from it that the foliage leaves are borne. The inflorescence is cymose. *Potentilla comarum* will serve as an alternative example (Fig. 426, *B*). The flower consists of:

Calyx, sepals 5, polysepalous, seated at the margin of the widened receptacle. Between the sepals are five additional green lobes, forming what is called an

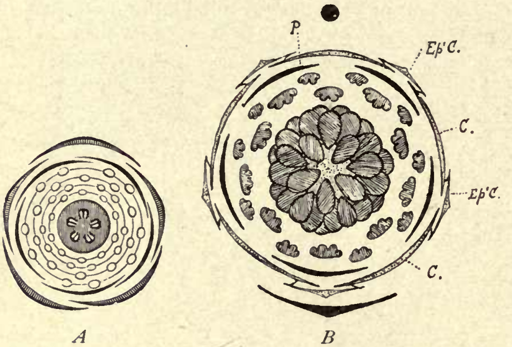


FIG. 426.
A, diagram of Apple. (After Eichler.) *B*, diagram of *Potentilla comarum*. *C*, diagram of Cherry. (After Eichler.)

epicalyx, believed to represent the fused pairs of stipules of the sepals, the vegetative leaves being stipulate. (The number of sepals in cultivated strawberries may be more than five.)

Corolla, petals 5, polypetalous, alternating with the sepals.

Androecium, stamens indefinite, free, perigynous. They are arranged with some regularity in whorls; the outermost is of 10, representing five stamens which have undergone fission.

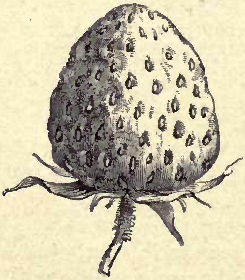


FIG. 427.
Succulent receptacle of Strawberry. (After Figuier.)

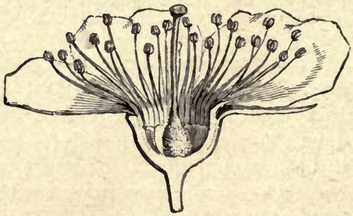


FIG. 428.
Vertical section of flower of the Peach, as an example of a perigynous flower. (After Figuier.)

Gynoecium, carpels indefinite, apocarpous superior, seated on the spherical receptacle. Style springing from the side of each ovary, which contains only one ovule.

Fruit. A number of dry nuts seated on the receptacle, which has become distended and succulent, while the calyx is persistent as the "hull" (Fig. 427).

Pollination. The flowers are conspicuous by their white petals, and honey is secreted on the receptacular cup between stamens and carpels. They are slightly protogynous. The result of repeated insect visits will thus be a probability of cross-pollination, though self-pollination is also possible.

(28) The flower of the Dog Rose (*Rosa canina*, L.) is constructed on a plan similar to that of the Strawberry, but without the epicalyx. The chief difference is in the receptacle, which instead of being convex with the carpels carried up on the hemispherical axis, is hollowed into a sunken cavity. This encloses the numerous bristly carpels, while their stigmas project above. When mature the receptacle becomes succulent as in the Strawberry, forming the "hip," with the nutlets or true fruits within.

(29) The Cherry (*Prunus cerasus*, L.) has a construction of the flower like that of the Rose, but with only one carpel borne in the hollow, cup-like receptacle (Fig. 428). It consists of:

Calyx, sepals 5, inserted upon the margin of the cup-like receptacle. The odd sepal is posterior.

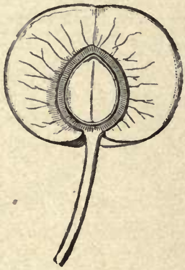


FIG. 429.
Drupe of Cherry. (After Figuier.)

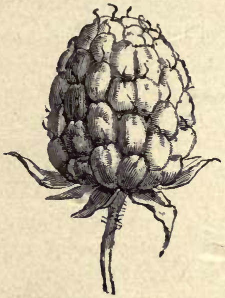


FIG. 430.
Grouped drupels of the Raspberry. (After Figuier.)

Corolla, petals 5, polypetalous, alternating with the sepals.

Androecium, stamens indefinite, free, perigynous, *i.e.* inserted on the margin of the receptacular cup.

Gynoecium, carpel 1, superior. The swollen ovary contains two ovules.

Fruit, a drupe. The receptacular cup here dries up, and falls away. The wall of the ovary differentiates into a superficial skin, a middle region of succulent pulp, and an inner stony layer. The stone of the mature cherry contains as a rule only one kernel, which is the exalbuminous seed, developed from one of the ovules. Sometimes, however, both are matured. The *Drupe* thus constructed is the type of fruit of Plums, Apricots, Peaches, etc. (Fig. 429).

Pollination. The Cherry flower is not highly specialised. Anthers and stigmas ripen simultaneously. Honey is secreted on the hollow surface of the cup. It is visited by various short-lipped insects.

The variability of Rosaceous flowers is illustrated by such examples. A striking feature is the diversity of origin of the succulent pulp, which gives value to their fruits. In the Strawberry it arises from the convex receptacle; in the Rose from the concave receptacle; in the Apple and Pear partly from the receptacle, partly from the carpels; in the Raspberry it is from the middle layer of the tissue of the very numerous carpels (Fig. 430); in the Cherry and Plum from the corresponding tissue of the single carpel.

ORDER: LEGUMINALES.

This is one of the largest and most important families of Plants, and it is cosmopolitan. It is characterised by its gynoecium, which consists of a single carpel, ripening as a Legume, or Pod, as in the Pea. It is divided into three Families: the *Mimoseae*, which are the most primitive, having flowers of radial symmetry, as in *Mimosa* and *Acacia*; the *Caesalpineae*, which have zygomorphic flowers, as in the Tamarind, or *Cassia*; and the *Papilionaceae*, or Pea-flowers. The last of these only are represented in the British Flora. The Order yields most varied products of importance: food-stuffs, timbers, drugs, and dyes, etc.

Family: PAPILIONACEAE. *Examples:* TREFOIL, PEA.

(30) The Bird's Foot Trefoil (*Lotus corniculatus*, L.) forms many straggling branches from a central root-stock. The leaves have green "stipules" which are really basal pinnae, and three distal lobes, hence its name. The flowering branches are leafless, but bear distally a leafy bract and a radiating group of flowers. Each flower is strongly zygomorphic, its plane of symmetry being vertical and median, as it is in all of the Papilionaceae (Fig. 431). It is composed thus:

Calyx, sepals 5, gamosepalous, inferior, the odd sepal being anterior. The calyx-tube gives mechanical support to the internal parts, and is slightly widened in a perigynous manner.

Corolla, petals 5, polypetalous, inserted separately on the slightly widened receptacle, *i.e.* perigynous. The petals alternate with the sepals. The posterior petal is the large vexillum, or standard; the two lateral are the alae or wings, which invest the anterior carina, or keel. The latter is formed from two obliquely anterior petals, inserted by separate stalks, but fused distally, so as to enclose the stamens and carpel.

Androecium, stamens 10, perigynous: nine are united by their stalks into a tube; the tenth, which is posterior, is separate to its base. The anthers are completely enclosed in the carina.

Gynoecium, carpel 1, apocarpous, superior. It is a pod, containing numerous ovules, with placentation on the posterior margins. The style is longer than the stamens, and bears a capitate stigma. The pod is almost surrounded by the united filaments, but access to the honey-secretion, which is on the enlarged receptacle round its base, is gained through the slits right and left of the separate stamen. The fruit when ripe is a dry pod, splitting longitudinally into halves.

Pollination. The mechanism of the flower is elaborate, and secures cross-pollination notwithstanding the close relation of anthers and stigma, which are both enclosed in the funnel-like carina. For the stigma is not receptive until it has been rubbed, and remains infertile till the insect-visitors, which are bees, arrive. Searching for nectar, and guided by the converging red lines on the standard, the bee alights on the projecting wings; its weight is transmitted by their interlocking surfaces to the keel, which is thus depressed, and yields. The stiff stamens and carpel do not yield, and so first the stigma, and then the anthers with their pollen project through a pore which is left open at the tip of the keel. When the weight of the bee is removed the keel rises, and the stamens and stigma are again enveloped, and are ready for a fresh insect visit. The effect of such visits will be, *first*, to rub the stigma, and make it receptive, while as it emerges first from the keel it receives any pollen brought from other flowers by the bee; *second*, to deposit a fresh supply of pollen on the insect. A cross-pollination is thus a virtual certainty.

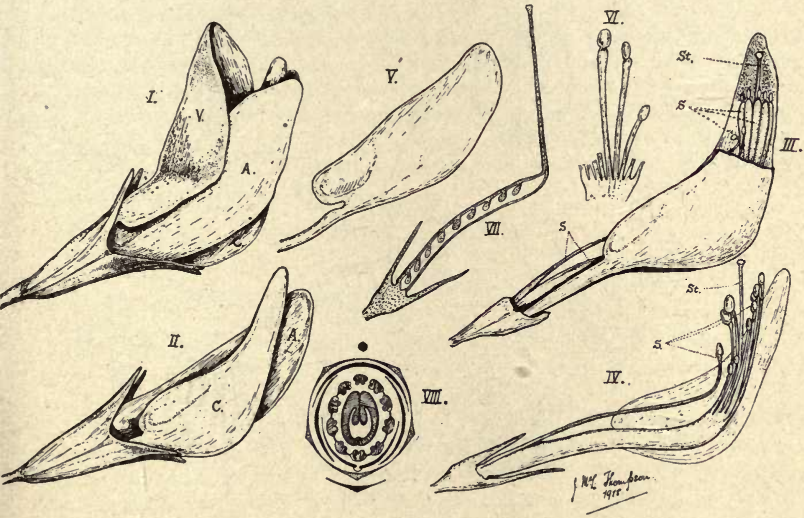


FIG. 431.
Flower of *Lotus corniculatus*, L. I. flower complete. II. with vexillum removed. III. with alae and part of carina removed. IV. carina slit longitudinally. V. one of the alae. VI. stamens of different length. VII. carpel in section. VIII. floral diagram. *s* = sepals; *v* = vexillum; *A* = alae; *c* = carina; *s* = stamens; *st* = stigma.

(31) The flower of the Garden Pea (*Pisum sativum*), may be taken as an alternative type, the construction being essentially the same as in *Lotus*, though differing slightly in details of its mechanism. The weight of the visiting insect depresses the interlocking wings and keel as before; but the latter is closed only along the anterior margin, so that when it is depressed the stiffer stamens and carpel rise out of the boat-like keel, and come in contact with the lower surface of the insect. The style bears a brush of hairs, which, as it rises, sweeps out the pollen on to the insect's body; but the stigma reaches its body first, and receives thus such pollen as it may have brought. The flower is elastic and recovers, making successive visits possible. The mechanism is less precise than in *Lotus*, but still very effective. It requires a strong insect, and in absence of cross-pollination self-pollination is possible.

These examples serve to illustrate the exact mechanism of the Papilionaceous flower, and the way in which slight differences may affect the process of their pollination.

ORDER: UMBELLALES.

Family : UMBELLIFERAE. *Example :* COW PARSNIP.

(32) The Cow Parsnip (*Heracleum sphondylium,* L.) is a coarse perennial herb, with massive storage stock, which sends up the annual leafy and flowering shoot. The stem is hollow and fluted, and bears alternate leaves with broad sheathing base, and irregularly cut lamina. The main inflorescence is terminal, but others may arise in the axils of the upper leaves. It is a compound umbel (p. 228, Fig. 176). The flowers are individually small, but many being

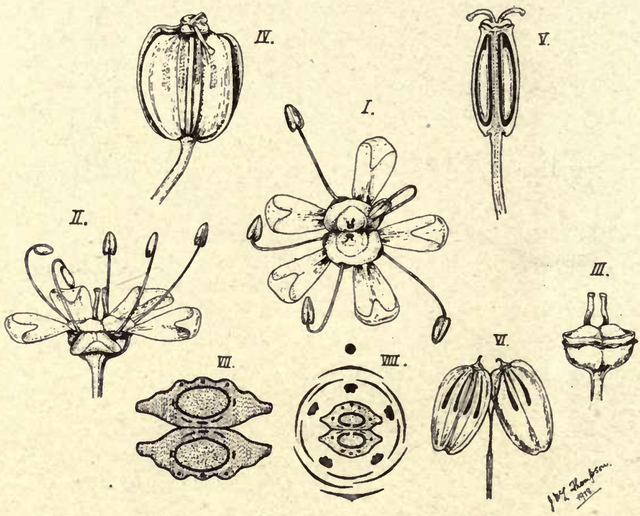


FIG. 432.
Heracleum sphondylium. **I. whole flower seen from above. II. the same seen from the side. III. gynoecium. IV. fruit. V. ditto in section. VI. mature fruit with mericarps separate. VII. fruit in transverse section. VIII. floral diagram.**

grouped together, and all at the same level, the aggregate inflorescence becomes a conspicuous feature. Each flower is borne upon a slender hairy stalk, which widens out just below the flower itself into a flattened green body. This is the inferior ovary, and the flower is *epigynous* (Fig. 432). Care should be taken to select perfect flowers for observation, as the parts fall away early. The flower consists of:

Calyx, sepals 5, superior, present as minute teeth visible between the petals. The odd sepal is posterior.

Corolla, petals 5, polypetalous, free, superior. Each is notched at the free edge. In the marginal flowers the petals are unequal, the outermost being the largest.

Androecium, stamens 5, free, epigynous, alternating with the petals ; bent inward in bud, but straightening when mature.

Gynoecium, carpels 2, syncarpous ; stigmas 2, styles widening downwards into two yellowish green nectaries. Ovary inferior, bilocular, with one pendulous ovule in each loculus.

Fruit, a flattened oval body, which matures dry. When ripe it splits into two halves (mericarps), attached at first by a slender middle column, from which they later break away, and are readily carried by the wind. Each mericarp contains a single albuminous seed, and is marked by elongated oil-glands, four on the outer and two on the inner flattened sides.

Pollination. The aggregate inflorescence attracts the attention of insects from a distance : the slight zygomorphy increases its effect. It is visited by various insects, the exposed honey being accessible alike to short-tongued and long-tongued. The individual flowers are *protandrous*, the stamens often falling before the stigmas are mature. Cross-pollination is probable by insects crawling from flower to flower, but self-pollination is still possible.

There is in the Cow Parsnip, but still more in other Umbelliferae, a partial separation of the sexes in space as well as in time ; since the pistil is degenerate in the later-formed flowers, they are practically male. That is seen markedly in *Astrantia* and in *Myrrhis*. The condition is described as *andro-diclinous*, and clearly it will promote cross-pollination, while it also secures the pollination of those hermaphrodite flowers which are formed late, and are protandrous.

DICOTYLEDONEAE—SYMPETALAE.

Those Dicotyledons which have their petals united, that is sympetalous or gamopetalous, are held to show in this respect a position in advance of the Polypetalous types. A further character which they have in marked degree is that their flowers are strongly cyclic, and the number of parts more definite than in flowers of more primitive construction. They are divided into two series on the broad feature of the number of the whorls in which their parts are arranged. Those with five whorls have the general formula, S. n, P n, A. $n + n$, G. $n -$, and they are styled the *Pentacyclicae*. Those with only four whorls have the general formula, S. n, P. n, A. n, G. $n -$, and they are styled the *Tetracyclicae*. The number of the carpels is usually below the typical number (n). The number of the stamens is also frequently less than (n), or $n + n$, especially in those flowers where the pollination-mechanism is specialised.

(*a*) *PENTACYCLICAE.*

ORDER : BICORNES.

Family : Ericaceae. *Example :* Cross-leaved Heath

(33) The Cross-leaved Heath (*Erica tetralix*, L.) is a shrubby moorland plant, mycorhizic like the rest of the family, bearing minute stiff leaves, studded with red, stalked glands. The margins of the leaves are reflexed, so that the lower stomatal area is concave, and more or less closed. All these features are xerophytic.

The flowers are borne in dense racemes, and are pendulous on pedicels bearing two bracteoles (Fig. 433). They consist of :

Calyx, sepals 4, polysepalous, inferior, glandular.

Corolla, petals 4, gamopetalous, inferior, globose, with a narrow opening, through which the capitate stigma projects.

Androecium, stamens 4 + 4, free, hypogynous, with curved filaments; anthers dehiscing by two distal pores, which face downwards. From the base of each anther two divergent spurs project outwards to the inner surface of the corolla.

Gynoecium, carpels 4, syncarpous, superior, style elongated, with capitate stigma. Ovary with 4 loculi, ovules minute, numerous, on an enlarged axile placenta. Honey-disc round the base of the hairy ovary.

Fruit, a loculicidal capsule, from which the minute seeds are shaken by wind.

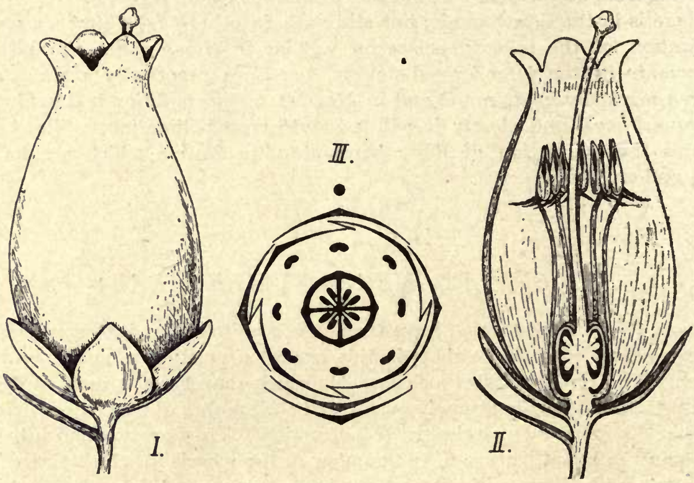


FIG. 433.
Erica tetralix. I. whole flower from outside. II. flower in section. III. floral diagram.

Pollination is by bees, which hang on to the pendent flowers. The bee first touches the sticky stigma, depositing pollen it may have brought from another flower; then inserting the proboscis, it collides with the spurred stamens, shaking out a shower of dry pollen. Thus there is a high probability of cross-pollination, though self-pollination is possible by some falling upon the stigma of the same flower. The gamopetalous corolla with narrow mouth, and the spurred stamens exclude small thieving insects.

(34) Compare the Bilberry (*Vaccinium myrtillus*, L.), in which the floral structure is essentially the same, but the ovary is here inferior. In this genus, and in the Ericaceae generally, there is frequent *meristic variation*, the flowers being either tetra-merous or penta-merous.

ORDER: PRIMULALES.

Family: PRIMULACEAE. *Example*: COMMON PRIMROSE.

(35) The Primrose (*Primula vulgaris*, Huds.) is a perennial with its stock covered with old leaf-bases, and ending in a rosette of leaves of the current

year. The flowers are borne singly in the axils of bracts, which succeed the foliage leaves. There are two types of flower which are borne on distinct plants: "pin-eyed," with the stigma occupying the centre of the flower, and "thrum-eyed," where its place is taken by five anthers. It will be seen, however, that in number and arrangement of the parts both are alike: the difference is one of proportion of development of the parts (Fig. 434). For convenience a "pin-eyed" flower may be taken first; it consists of:

Calyx, sepals 5, gamosepalous, inferior, forming a tube supporting the corolla. The odd sepal is posterior.

Corolla, petals 5, gamopetalous, inferior, alternating with the sepals, and

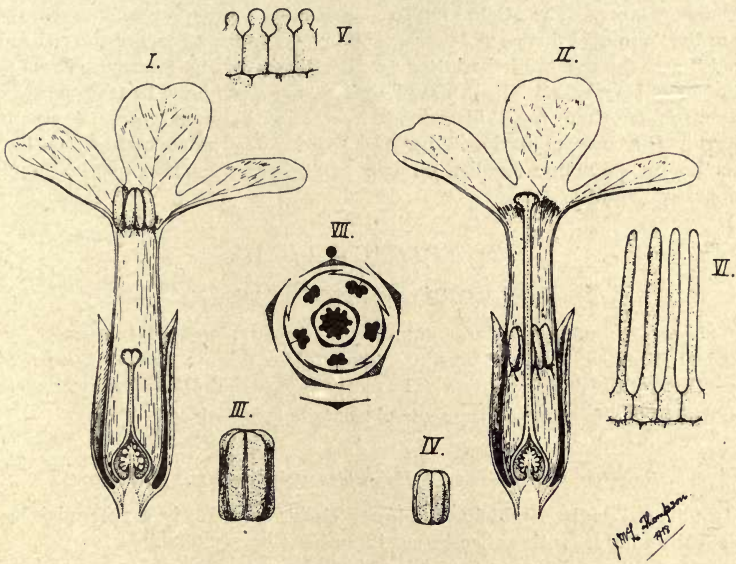


FIG. 434.

Primula vulgaris. I. short-styled type of flower in section. II. long-styled type, ditto. III. pollen of short-styled. IV. of long-styled types. V. stigmatic papillae of short-styled. VI. of long-styled type. VII. floral diagram.

forming a long narrow tube below, with five lobes diverging at right angles from it.

Androecium, stamens 5, epipetalous, inserted with very short filaments half-way up the tube of the corolla, and opening inwards. Note that the stamens are opposite the petals (anti-petalous).

Gynoecium, carpels 5, syncarpous, superior; style elongated so as to carry the pin-headed stigma to the throat of the corolla. Ovary turgid, unilocular; ovules numerous, placentation axile.

Fruit, a capsule opening distally by ten teeth, which become reflexed. The number five of the carpels is inferred from comparison with other flowers, and from the parts of the Primrose itself. The ten teeth of the fruit support this view. The anti-petalous position of the stamens, and the number (n), instead of ($n+n$), suggests that five sepaline stamens are abortive: this conclusion is supported by the fact that in *Samolus, Lysimachia*, etc., five small staminodes are present in the place where the missing stamens should be. The family shows meristic variation, the whorls varying in number of parts from four to nine. *Trientalis* and *Lysimachia* are specially variable.

Pollination. Compare first the "thrum-eyed" type of flower. The parts are numerically the same as in the "pin-eyed"; but the style carries the stigma only half-way up the corolla-tube, corresponding in level to the stamens of the "pin-eyed." The stamens are inserted at the throat of the corolla, corresponding in level to the stigma of the "pin-eyed." The effect of this "dimorphism" is to increase the probability of intercrossing as a consequence of repeated visits from bees to the two types of flower, which are borne on different plants. The sticky pollen deposited on the proboscis of the bee from the "pin-eyed" type will correspond in level to the stigma of the "thrum-eyed," and the pollen of the latter to the stigma of the former. These are what have been called "legitimate" crosses, and they have been shown to be more prolific than the "illegitimate" crosses, between parts of unequal length. But self-pollination is not precluded. The gamopetalous corolla is effective in excluding smaller insects, while bees are attracted by honey, colour, and scent.

(*b*) *TETRACYCLICAE.*

ORDER: PERSONATAE.

This Order includes a large number of showy plants of temperate and tropical climates, with tetracyclic, gamopetalous flowers, having the general formula S. 5, P. (5), A. 5, G. $(\underline{2})$. The ovary is superior, and bilocular, and the number of ovules borne on the axile placenta is usually large.

Family: SOLANACEAE. *Examples:* NIGHTSHADE, POTATO.

(36) The Deadly Nightshade (*Atropa Belladonna*, L.) is a perennial herb of shrubby habit, with entire leaves having a clammy glandular surface. It bears its flowers solitary in the axils of leafy bracts. The whole inflorescence, which is cymose, starts with a single terminal flower, below which strong branches develop, the ultimate branchings of which are complicated by adhesions. The flower consists of:

Calyx, sepals 5, gamosepalous, inferior; the odd sepal is posterior.

Corolla, petals 5, gamopetalous, inferior, alternating with the sepals; very slightly zygomorphic.

Androecium, stamens 5, hypogynous, epipetalous; filaments curved.

Gynoecium, carpels 2, syncarpous, superior, placed obliquely to the median plane; style elongated, stigma capitate, ovary bilocular, ovules numerous, placentation axile. A honey-disc surrounds the base of the ovary.

Fruit, a large black berry, surrounded by the persistent green calyx. Seeds albuminous, embryo curved.

Pollination. The colour and honey-secretion offer attractions to bees, especially humble-bees, while the gamopetalous corolla and the stiff hairs at the base of the filaments tend to exclude small crawling insects. The stigma and anthers mature almost simultaneously. The stigma projects beyond the curved stamens, thus there is a probability of cross-pollination from visits from humble-bees, but the flower is not highly specialised.

(37) The Potato (*Solanum tuberosum*, L.) is an herbaceous plant that reproduces itself by tubers (Fig. 138, p. 185). But it commonly flowers also in cymose inflorescences, which are without bracts. The flowers of the cultivated varieties are apt to show abnormalities. The normal structure is

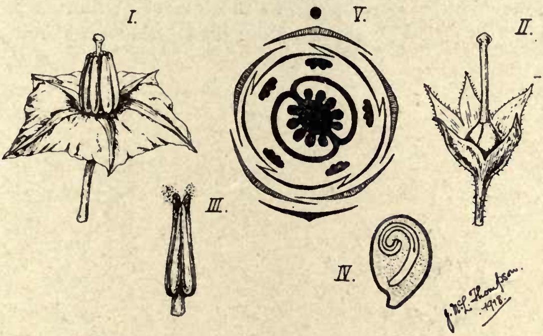


FIG. 435.
Solanum tuberosum. I. flower. II. pistil, and persistent calyx. III. stamen with porous dehiscence. IV. seed in median section. V. floral diagram.

like *Atropa* in number and arrangement of parts. But the corolla is wheel-shaped, and expanded in a vertical plane, while the five projecting stamens open by terminal pores (Fig. 435). The stigma projects beyond them. There is no honey-secretion. The native habitat is South America. The arrangement of the flower might lead to crossing if the suitable insects were present, but here insects rarely visit the flowers. Self-pollination is possible, and fruit is often set. The fruit is a berry.

ORDER: PERSONATAE.

Family: SCROPHULARIACEAE. *Examples:* FIGWORT, SPEEDWELL.

(38) The Figwort (*Scrophularia nodosa*, L.) is a common plant of moist soil, with upright four-angled stems bearing decussate leaves, and terminating in lax cymose panicles of tawny purplish flowers. They are zygomorphic, and strongly protogynous (Fig. 436). Each flower consists of:

Calyx, sepals 5, slightly gamosepalous, inferior. The odd sepal is posterior.

Corolla, petals 5, gamopetalous, inferior; two-lipped.

Androecium, stamens 4, epipetalous; the fifth posterior stamen represented by a prominent staminode below the upper lip.

Gynoecium, carpels 2, syncarpous, superior, antero-posterior; style elongated stigma capitate. Ovary bilocular, with numerous ovules on an enlarged axile placenta. A yellow honey-disc surrounds the base of the ovary. Fruit a dry capsule, which splits septicidally, and liberates the numerous albuminous seeds, with straight embryos.

Pollination. The tawny colour of the flower attracts wasps, which are the pollinating agents. The flowers are strongly protogynous. While the stamens are still tightly packed in the globose corolla, the stigma protrudes so as to meet any visiting insect, and receives any pollen he may bring. Later it is strongly recurved, and the stamens then straighten their filaments, carrying their anthers outwards, partly blocking the lower side of the corolla-tube. They will thus deposit their pollen on the ventral surface of the visiting insect, conveniently for transfer to the stigma of flowers in the earlier female stage. The posterior stamen from its position could not do this: it

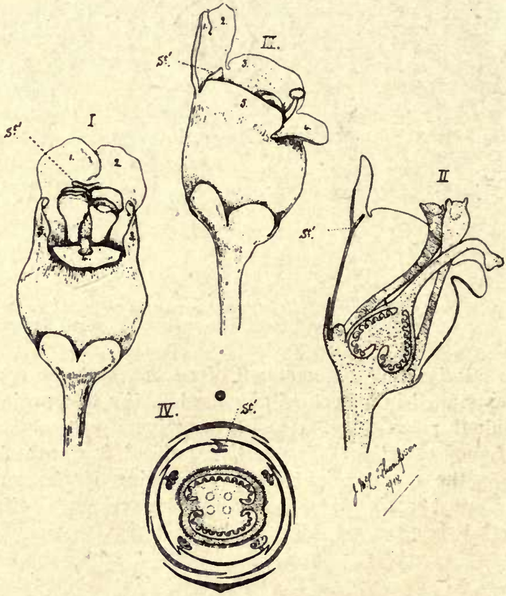


FIG. 436.
Scrophularia nodosa. I. flower in anterior view with stigma removed, and stamens dehiscent (late stage). II. same in section. III. flower seen laterally with projecting stigma (early stage). IV. floral diagram.

is superfluous, and is reduced to a staminode. Cross-pollination is thus highly probable, but self-pollination is possible by pollen falling from the anthers upon the still receptive stigma.

The Foxglove (*Digitalis purpurea*, L.) has a similar structure, but its wide bell is suitable for humble bees, the pollen being deposited on their backs. The flowers are here protandrous. Cross-pollination is probable, but self-pollination is still possible. Comparison of the Foxglove with the Figwort shows how, with the same plan of floral construction, there may be differences in the detail and in the agent of cross-pollination.

(39) The Germander Speedwell (*Veronica Chamaedrys*, L.) is a common perennial of road-sides and banks. It has long ascending shoots bearing decussate leaves. The racemose inflorescences arise in the axils of the upper

leaves. Each flower has a slender stalk, and consists of the following parts:

Calyx, sepals 4, slightly gamosepalous, inferior. Though the number appears to be four, comparison with other species of *Veronica*, and with other related plants, such as the Foxglove, shows that a fifth sepal, which should be median and posterior, is here wanting.

Corolla, petals apparently four, gamopetalous, inferior, alternating with the sepals and forming a wheel-shaped (rotate) corolla, which readily falls away in one piece. Comparison with related plants shows that the large

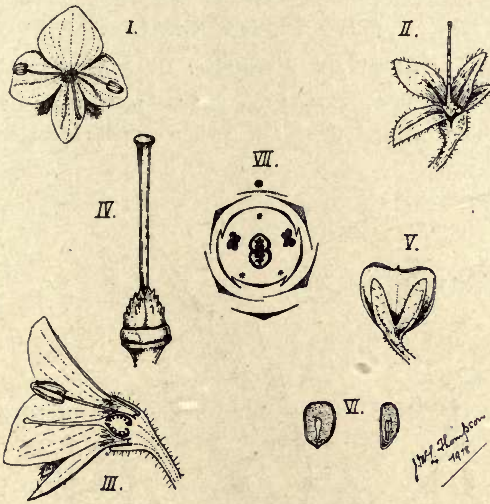


FIG. 437.
Flower of *Veronica chamaedrys*, typically pentamerous: but the posterior sepal is abortive: the two obliquely posterior petals are fully fused to form apparently one; only the two obliquely posterior stamens are developed.

posterior petal is really the equivalent of two obliquely posterior petals fused together. In front view the petals are marked by lines, or honey-guides, converging to the centre of the flower.

Androecium, stamens 2, epipetalous, diverging widely right and left. Comparison shows that these correspond to the two obliquely posterior stamens, while those obliquely anterior are abortive, as well as the median posterior stamen (Fig. 437).

Gynoecium, carpels 2, antero-posterior, syncarpous, superior. The single style projects between the diverging stamens, and bears a capitate stigma. Ovary bilocular, ovules numerous, placentation axile.

Fruit, a dry capsule.

Pollination. The flower is a specialised and reduced example of the Scrophulariaceae. The change from a pentamerous to an apparently tetramerous type follows from the abortion of the posterior stamen, which leads to abortion of the posterior sepal and fusion of the two obliquely posterior petals. The obliquely anterior stamens are also abortive, not being necessary for effective pollination by flies. The rotate corolla is expanded in a vertical plane, with the style and two stamens projecting horizontally. The insect alighting on the flower gains a foothold by grasping the stamens, drawing them together so that they deposit pollen on the under surface of his body. On going to another flower the stigma receives this, before an additional supply from that flower can be deposited. The result is a high certainty of cross-pollination, with high improbability of self-pollination ; and it is effectively carried out without the three stamens that are abortive.

ORDER: VERBENALES.

Family: LABIATAE. *Examples:* DEAD-NETTLE, SAGE.

(40) The Labiatae are a very large Family including herbs and shrubs spread through warm and temperate regions, and characterised by their

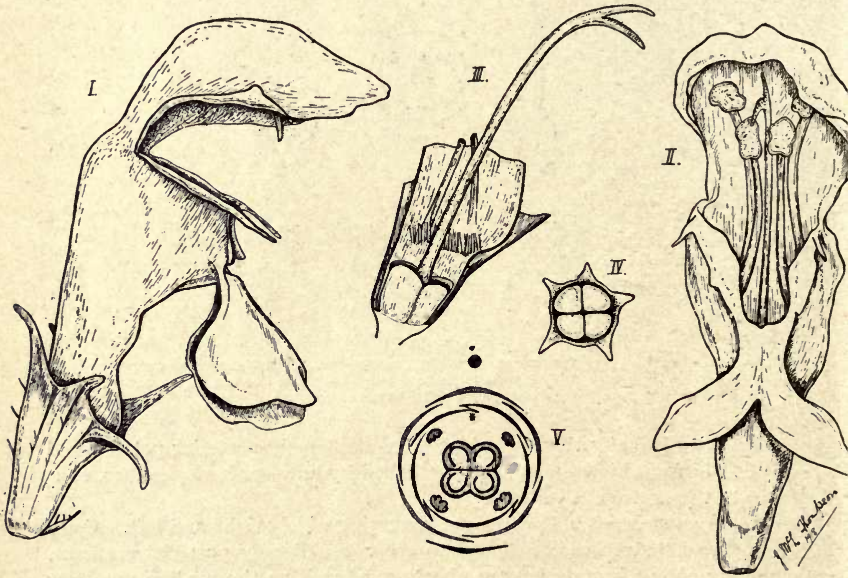


FIG. 438.

Lamium album. I. flower seen laterally. II. same in frontal view. III. dissection showing ovary and style, and the base of the corolla-tube, with insertion of stamens, and fringe of hairs. IV. ovary as seen from above. V. floral diagram.

four-angled stamens and decussate leaves. They have often an aromatic smell: Mint, Sage, and Lavender are examples. Their floral structure is very constant. The flowers are either solitary or in axillary cymes. The White Dead Nettle (*Lamium album*, L.) illustrates the leading features. Its flowers, which are in crowded "verticillasters," show their cymose arrangement by the fact that the flower directly in the axil of the leafy bract opens first, and those right and left successively later. Each flower is strongly zygomorphic, with its median plane vertical (Fig. 438). It consists of:

Calyx, sepals 5, gamosepalous, inferior, odd sepal posterior.

Corolla, petals 5, gamopetalous, inferior; strongly two-lipped. One large petal forms the anterior lower lip, two smaller petals guard the entrance to the tube laterally, the upper lip forms a hood, composed of two obliquely posterior petals. The corolla is easily removed in one piece, its tube is narrow below, but widens upwards.

Androecium, stamens 4, epipetalous. The fifth posterior stamen is absent, its place being inconveniently behind the style. The anthers, of unequal length, and opening downwards, lie below the hood of the corolla. In this Family sometimes the outer, sometimes the inner pair are the longer.

Gynoecium, carpels 2, syncarpous, superior, antero-posterior; style elongated; stigma two-lipped, lying between the pairs of anthers, with lobes widely divergent, the anterior lobe directed downwards. The ovary 4-partite, with one anatropous ovule in each. It is really bilocular, with two ovules in each loculus; but it becomes "falsely" quadrilocular by intrusion of a septum between each pair of ovules. Nectaries are found at the anterior base of the ovary. The nectar accumulates in the narrow lower part of the corolla-tube, protected by a ring of hairs which grow inwards from the tube of the corolla just above the ovary.

Fruit, four dry nutlets, two being derived from each carpel. They remain till shed, enclosed by the persistent calyx.

Pollination is by bees, which alight on the lower lip of the corolla and insert the proboscis into the tube. The bee's body fills the space between the upper and lower lips, so that its back presses against the stamens and stigma. The anterior lobe of the stigma projects further downwards than the stamens, so that it first touches the back of the bee, receiving pollen if he has brought any from another flower. He then receives pollen from the anthers which open downwards. The flower is homogamous, that is, the stigma is receptive at the time when the pollen is shed. Self-pollination is therefore possible, but there is a high probability of cross-pollination.

(41) The Dead Nettle is highly specialised, and deposits the pollen on a limited area of the insect's body; but a still higher degree of specialisation is seen in *Salvia pratensis*, or other species. The plan of the flower is the same as in *Lamium*, but, as the mechanism is more precise, sufficient probability of pollination can be secured with greater economy of pollen than in other Labiatae (Fig. 439). Only the two obliquely anterior stamens are matured, the posterior are represented by minute staminodes, or are quite abortive. The anthers of the two well-developed stamens have the "connectives" between the anther-lobes elongated, so that they are separated about half an inch. Each anther is affixed midway on the short stout filament of the stamen by a flexible joint, so as to be able to move like the lever of an Egyptian well. One of the lobes is directed forwards, and this develops normal pollen; the other is directed backwards and develops as a sterile knob. This is so placed as to block the entrance to the corolla-tube, while the fertile lobe rests under the hood of the corolla. The flower is strongly protandrous, the style being hidden, and the stigma-lobes appressed at the time of shedding of the pollen.

If a large insect, perching on the lower lip of the flower of Sage, inserts its proboscis, the sterile lobes will be pressed upwards, and this will cause the fertile lobes to descend, depositing the pollen over a definite area of the insect's back. In older flowers that have already shed their pollen, the style elongates :

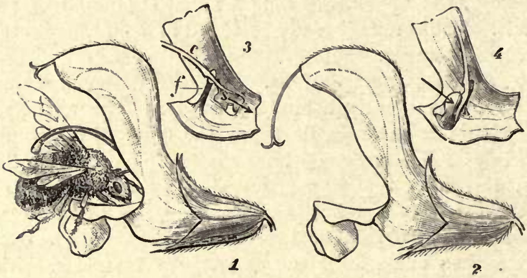


FIG. 439.

Pollination of *Salvia pratensis*. 1, Flower visited by Humble Bee, showing the projection of the curved connective from the helmet-shaped upper lip, and the deposit of the pollen on the back of the Bee. 2, older flower, with connective withdrawn and elongated style. 4, the staminal apparatus at rest, with connective enclosed within the upper lip. 3, the same when disturbed by the entrance of the proboscis of the Bee in the direction of the arrow. *f* = filament. *c* = connective. *s* = the obstructing half of the anther, which produces no pollen. (After Strasburger.)

its lobes diverge and take such a position that the stigma touches that region of the insect's body which received the pollen from the younger flowers. Cross-pollination thus follows on repeated visits to flowers of various ages ; and it is effected with a high degree of certainty, though in each flower only two half-anthers are fertile. Economy of pollen follows on perfection of the mechanism.

ORDER : SYNANDRAE.

Family : COMPOSITAE. *Examples :* OX-EYE, DANDELION, CENTAURY.

The Family of the Compositae consists mostly of herbs. It is of world-wide distribution, and is the largest Family of Flowering Plants. It is characterised by having the gamopetalous flowers collected into capitula, or heads. Each *head* is surrounded by a common *involucre* of protective bracts. The

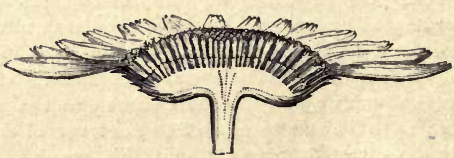


FIG. 440.

Inflorescence of Daisy : a capitulum. (After Figuier.)

whole head is equivalent biologically to a single flower, and behaves as such, though morphologically it is a *closely packed, spicate inflorescence.* The Dandelion and Daisy are familiar examples (Fig. 440). The structure of the individual flower is already known in the case of the Sunflower, by the study of its development (Chapter XIII., p. 239, Fig. 188). Each flower is there seen in the normal position, *i.e.* in the axil of a bract; it consists of 5 petals, 5 stamens, and 2 carpels. The transverse section of the flower approaching maturity shows these parts arranged as in a floral diagram. The odd petal is anterior; the stamens alternate with the petals, and the carpels are antero-posterior (Fig. 188, viii.). The ovary is inferior, unilocular, and contains one ovule. This structure is fundamental for all Compositae (Fig. 441).

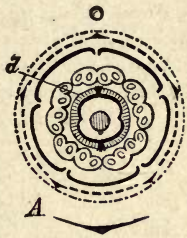


FIG. 441.
Floral diagram for Compositae. (After Eichler.)

As in similarly crowded inflorescences (for instance the cyathium of the Spurges, p. 515), the crowding brings with it reduction of the individual flowers, but it does not go so far in the Compositae as in the Spurges. The most usual modification is the reduction of the calyx, its protective function having devolved upon the involucre. Sometimes it is absent, as in the Daisy; or it may be represented by two or three teeth, as in *Bidens* (Fig. 238, *E*). But most frequently it is developed as a means of fruit-dispersal, taking the form of a "pappus" composed of bristles, which spread like a parachute (Fig. 234, p. 290). The bract subtending each flower is often abortive, as in the Dandelion and Daisy. The flowers themselves though typically hermaphrodite are liable to become unisexual by abortion. These are all features of reduction, following on the aggregation of the flowers in the compact inflorescence.

The florets may develop in three different ways, though all are fundamentally of the same construction, having the general formula, S, (5, or 0 or x), P. 5, A. 5, G. $(\overline{2})$. The first type is radially symmetrical, with five equal petals. This is probably the original type, and is characteristic of the *florets of the disc* (Fig. 442, III., IV.). A second type is seen in the *ray-florets* (Fig. 442, V.), in which the corolla is tubular below, but the three anterior petals are elongated into a long strap-shaped ray, as shown by the three distal teeth; the two obliquely posterior are reduced or absent. These ray-florets are frequently female, or neuter. A third type is the *ligulate floret*, in which the corolla is split on one side, and all the five petals, as shown by the five distal teeth, are elongated into a strap-shaped ray; but here all five join in its formation (Fig. 444). According to the type of flower the Family is divided into two Subfamilies: (i) The *Tubuliflorae*, in which the flowers are all tubular, or the outer may be developed as ray-florets (Fig. 442). They have watery juice. Examples are the Groundsel, Daisy, Sunflower, and Centaury. (ii) The *Liguliflorae*, in which all the flowers are ligulate (Fig. 444). They have milky juice. Examples are Dandelion or Hawk-weed.

(i) *Tubuliflorae.*

(42) The Common Groundsel (*Senecio vulgaris*, L.) is one of the commonest weeds of cultivated ground. It is annual and herbaceous, with branched leafy stem, bearing a few heads drooping when young, erect when old. The single head, examined in full flower, shows a green involucre of bracts, the

outer short, the inner long, with black tips. These surround numerous tubular disc-florets. Ray-florets are usually absent. The single disc-floret consists of:

Calyx, represented by numerous bristles (pappus), rising from the top of the inferior ovary.

Corolla, petals 5, gamopetalous, superior, rather longer than the pappus. The five equal teeth are borne at the end of the corolla-tube, which is narrower below and widens upwards into a bell.

Androecium, stamens 5, epipetalous, alternating with the petals, inserted by five distinct filaments on the throat of the corolla-tube at the point where it dilates. Anthers united into a tube (syngenesious).

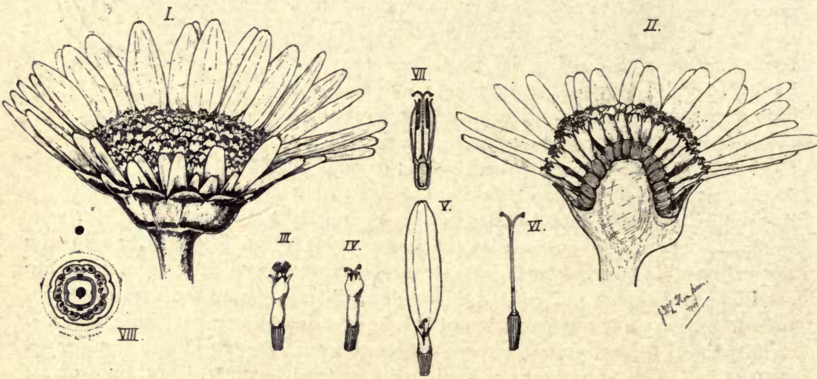


FIG. 442.

I. Whole capitulum of *Chrysanthemum*. II. same in median section. III. disc-floret in earlier (male) condition. IV. same in later (female) condition. V. ray-floret. VI. style and stigma. VII. disc-floret in section. VIII. floral diagram.

Gynoecium, carpels 2, syncarpous, ovary inferior, unilocular, with one anatropous ovule. Style elongated, bearing in fully matured flowers two antero-posterior lobes, which diverge beyond the tube of the anthers.

Fruit, a brown striated nut, bearing the wide-spread pappus at the tip, by means of which it is distributed by the wind.

Pollination. If several flowering heads be examined from above it will be seen that the flowers mature in *acropetal succession*, the oldest being outside. The corolla bursts, the syngenesious and introrse anthers protrude, and the pollen is driven out of them by the elongating style, the stigmatic lobes being still appressed; later these expand, exposing their inner receptive surfaces. The flowers are thus *protandrous*. There is honey-secretion in the corolla-tube, but the flowers are rarely visited by insects, and self-pollination is certainly common.

(43) The Ox-Eye Daisy (*Chrysanthemum leucanthemum*, L.), belonging also to the Tubuliflorae, is a common perennial of dry ground (Fig. 442). The capitulum is solitary on the end of a stem, which widens out to form the *general receptacle*. From its margin arises the involucre of bracts, with membranous margins. Within are numerous florets inserted on the receptacle, but without

any bracts subtending them. Centrally are the yellow florets of the disc, peripherally the ray-florets. Each disc-floret consists of :

Calyx, represented only by a rim round the upper limit of the inferior ovary. There is no pappus.

Corolla, petals 5, gamopetalous, superior.

Androecium, stamens 5, alternating with the petals, epipetalous, inserted by separate filaments upon the throat of the corolla, but with the anthers united laterally into a tube (syngenesious).

Gynoecium, carpels 2, antero-posterior, syncarpous. Ovary inferior, unilocular, containing a single anatropous ovule. Style elongated, and bearing up through the tube of the anthers the two lobes of the stigma, which diverge beyond it in the later stages of flowering (Fig. 442, vii.)

The white ray-floret consists of :

Calyx, as before.

Corolla, petals 5, gamopetalous ; tubular below, elongated above into a narrow strap-shaped ray representing the three anterior petals, the two posterior being here obsolete.

Androecium, absent.

Gynoecium, as before (Fig. 442, v.).

Fruit. Each flower produces a dry achene, which at maturity is shaken out from the protecting involucre. There is no pappus.

Pollination. The mechanism is here essentially the same as in Groundsel, but with addition of the attractive ray-florets. In the first flowering stage the disc-florets offer pollen ; in the second stage the expanded stigmas to the insects that are attracted by the colour and honey (iii. iv.) Any crawling insect will effect crossing. But if this fails self-pollination is also possible

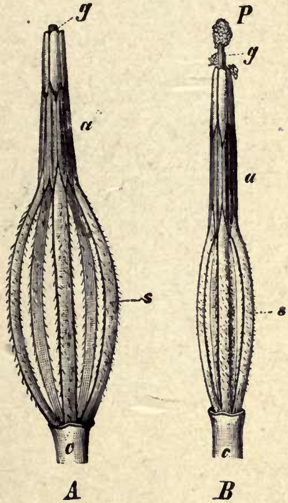


Fig. 443.
Stamens and style of *Centaurea*. *A*, in the unstimulated, *B*, in the stimulated state. The style in the latter projects beyond the anthers, and the pollen has been brushed out. (After Strasburger.)

(44) A third more elaborate type is seen in Cornflower (*Centaurea cyanus*, or *C. montana* will serve). The general structure is the same, but the ovoid head is tightly enclosed by the appressed bracts with brown margins. The receptacle is flat and bristly. The flowers are all tubular, but the *outermost are neuter*, and coloured, with long tubular two-lipped and 5-lobed corolla, and abortive stamens and ovary. The *inner* florets are *hermaphrodite*, and of the usual type, with pappus of short unequal bristles. The lower part of the corolla-tube is tubular and narrow, the upper is globose, bearing five distal lobes. The syngenesious anthers form a dark purple tube, with a terminal beak. The style bears below the stigma-lobes a ring of bristles, which acts like a sweep's brush upon the pollen. The flowers are protandrous as before. The *filaments* are curved and *sensitive, contracting on the stimulus of touch*. This is received by hairs radiating out from them ; honey is secreted at the base of the corolla (Fig. 443).

The insect visitors are most commonly bees. Inserting the proboscis into the tube of a floret with stigma not yet receptive, the filaments are stimulated; they straighten and contract, drawing the anther-tube downwards. The bristles of the style thus brush out the pollen at the moment the insect is there, and it is deposited on his body. If he then passes to a floret with stigmas expanded, cross-pollination is ensured. But self-pollination is also possible by

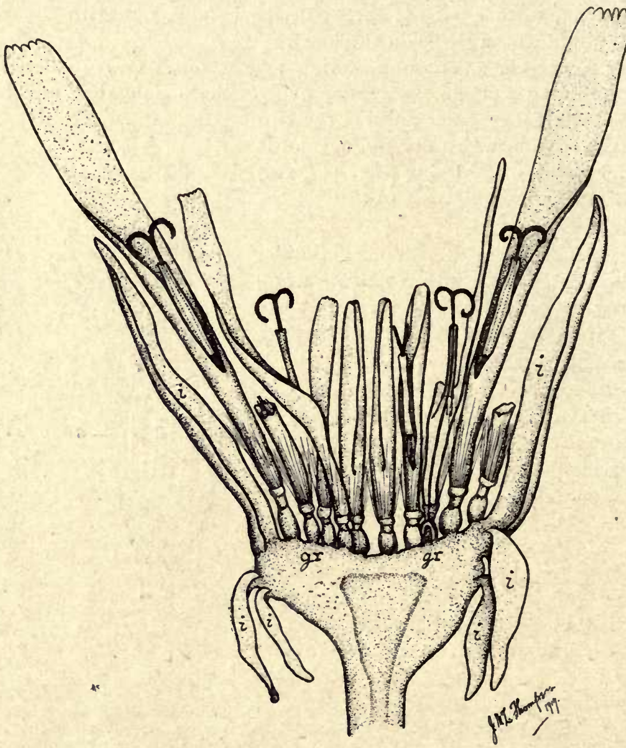


FIG. 444.
Head of Dandelion in vertical section. *i* = involucre. *gr* = general receptacle. See Text.

curvature of the stigmas to touch the pollen carried on the stylar brush. These examples show how differences of detail in the florets of the Tubuliflorae may be effective in pollination: the fundamental facts being a protandrous condition, and an aggregated inflorescence.

(ii) *Liguliflorae.*

(45) The Common Dandelion, or any Hawk-weed, will serve as an example. The Dandelion (*Taraxacum officinale*, Web.) is a perennial herb, with massive storage root, a rosette of radical leaves, and solitary, long-stalked heads. The tissues are traversed by branched latex-tubes containing milky-juice. The head consists of an involucre of bracts (Fig. 444, *i*), seated at the margin

of a naked, pitted general receptacle (*gr.*). Within are numerous *ligulate florets*, which are all alike, and have the same number and relation of parts as in the Tubuliflorae. But the split ligulate corolla shows by its five teeth at the distal end that it is composed of five petals.

The *pollination-mechanism* is founded on protandry. The elongating style sweeps out the pollen during the first stage of flowering; the stigma then expands and is receptive during the second stage. The heads expand in sunshine, and intercrossing is possible by many different insects. Self-pollination is also possible by the recurved stigmas coming in contact with pollen adhering to the style. It has, however, been found that in certain cases the fruit of the Dandelion can be matured without any pollination at all, even in buds from which the anthers and stigmas have been all cut away before flowering.

The *fruiting head* is the well-known Dandelion "clock." The individual fruit is a dry inferior achene or nut, attached by a long beak to the parachute-like pappus. These fruits are easily detached by wind, being exposed on the convex growth of the receptacle, owing to the curving back of the involucre (Fig. 445). They are thus scattered long distances by the wind. The success of the Compositae as a Family depends largely upon the certainty of each floret producing a good fruit, and on the effective dispersal of the fruit by the wind.

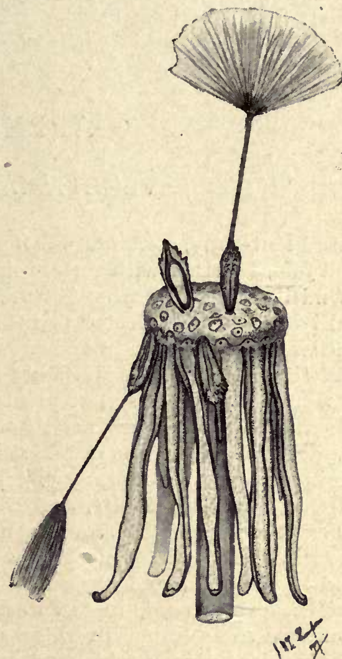


FIG. 445.

Fruit of Dandelion, with pappus as parachute.

APPENDIX B.

VEGETABLE FOOD-STUFFS.

THE Plant-body, containing as it does digestible proteids, carbohydrates, and fats, together with certain mineral salts, is a natural food for Man. Primitive Man used what Nature supplied. But with civilisation came cultivation of the selected plants which best met his needs. Continued cultivation led to improvement in quantity and quality of the crop; and though certain supplies are still drawn from natural sources, it is the cultivated plants that yield by far the greater proportion of the vegetable foods. They are so varied in origin, and in the parts used, that an exact scientific classification is difficult. They may be roughly grouped for practical study under four heads: as (i) Roots and Shoots, (ii) Legumes, (iii) Fruits, and (iv) Cereal grains. Naturally the parts where the material is stored compactly for the use of the Plant itself are those which are of most value to Man. It is to the roots and tubers, and to the fruits and seeds that he looks for his best supplies of food. On the other hand, in the kitchen garden profuse vegetation is encouraged so as to obtain in the shortest possible time a large quantity of succulent tissue, with the least proportion of woody fibre. Halophytes have provided many of the original stocks from which garden vegetables have sprung. The original sources of Cabbage, Sea-Kale, Beet, Asparagus, and Spinach were all coastal plants, while the Potato and Carrot are at home on marine sands.

The analysis of average samples affords some knowledge of the feeding value of each. The results of such analyses for a few of the vegetable foods in common use are given in the following tables, which have been extracted from König's *Die menschlichen Nährungs- und Genuss-Mittel*, and other sources. But there may be considerable variation from sample, and the figures should be held as a guide to an estimate of feeding-value rather than as any exact statement applicable to all cases.

The Potato (*Solanum tuberosum*, L. Solanaceae) grows abundantly on the sand of the sea-shore in the archipelago of S. Chili (Fig. 138, p. 185). At the time of the discovery of America its cultivation was practised with every appearance of ancient usage from Chili to New Grenada. It was introduced probably in the latter half of the sixteenth century into Virginia and North Carolina, and imported into Europe at the time of Raleigh's Virginian voyages, between 1580 and 1585, first by the Spaniards and afterwards by the English. The tubers, which are axillary buds specialised for storage and propagation, are deficient in fats, and contain little proteids. More than four-fifths of the organic substance is in the form of starch. Hence potatoes are used with meat and fats to make a well-balanced meal. The proteid is largely in the form of cubical crystalloids, located near to the corky rind, and thus liable to be removed by peeling the potato (Fig. 79, p. 110).

TABLE OF ANALYSES OF ROOTS AND SHOOTS.

N.B.—Vegetables used in the fresh state have a very high water-content. This must be taken fully into account in considering their value as foods.

Name.	Water.	Nitrogenous substances.	Fats.	Digestive carbohydrates.	Cellulose and lignin.	Ash.
Potato - - -	74·98	2·08	0·15	21·01	0·69	1·09
Beetroot - -	82·25	1·27	0·12	14·40	1·14	0·82
Parsnip - - -	79·31	1·32	—	16·36	1·73	1·28
Onion - - -	85·99	1·68	0·10	10·82	0·71	0·70
Carrot - - -	86·79	1·23	0·30	9·17	1·49	1·02
Turnip - - -	87·80	1·54	0·21	8·22	1·32	0·91
Cauliflower - -	90·89	2·48	0·34	4·55	0·91	0·83
Winter Kale - -	80·03	3·99	0·90	11·63	1·88	1·57
Celery - - -	84·09	1·48	0·39	11·80	1·40	0·84
Spinach - -	88·47	3·49	0·58	4·44	0·93	2·09
Lettuce - - -	94·33	1·41	0·31	2·19	0·73	1·03

The Beet (*Beta vulgaris* and *B. maritima*, L. Chenopodiaceae) grows wild on sandy shores in the Mediterranean region, extending northwards to our own coasts. Its originally slender root became fleshy from the effects of soil and cultivation, and Vilmorin has shown that it is one of the plants most easily improved by selection. It has been cultivated since before the Christian era. The fleshy root, characterised by repeated cycles of separate vascular strands, as seen in transverse section, contains cane-sugar in its sappy parenchyma. The analysis shows, for garden Beet, over 14 per cent.; but in specially selected and cultivated sugar-beets the percentage is very much higher. It has long been grown as a garden vegetable for winter use; but latterly it has become the chief European source of Sugar.

The Parsnip (*Pastinaca sativa*, L. Umbelliferae) ranks high as a nutritious vegetable. The original type is native in Britain; it has been cultivated since Roman times. The root, distended by cultivation, is apt to be fibrous on poor soils; but when well grown it contains a high percentage of digestible carbohydrates.

The Onion (*Allium cepa*, L. Liliaceae) was used as a condiment by the Egyptians, Greeks, and Romans. It appears to have originated from a wild species of the Middle East. The distended leaf-bases form a bulb containing a large deposit of sugar. But it is as a condiment that it is specially valued. Other species of *Allium* give Garlic, Shallots, Chives, etc.

The Carrot (*Daucus Carota*, L. Umbelliferae) is the enlarged root of the species native in Britain.

The Cabbage, Kale, Cauliflower, and Turnip (Cruciferae) are represented by many varieties. They may all be attributed to one or another of four Linnaean species, viz. *Brassica oleracea, napus, rapa,* and *campestris*. Some varieties are cultivated for their leaves, as Cabbages; or for their crowded inflorescences, as Cauliflower; or for the oil in their seeds, as Colza and Rape; others again for the fleshy swellings of the root, or lower part of the stem. In Turnips and Swedes the hypocotyl is swollen; in Kohl-rabi the epicotyl. All of these were ultimately of European or Siberian origin, and some of their ancestral forms grow wild on our coasts. Their cultivation was diffused in Europe before the Aryan invasion. The analyses show that their value as foods is not high, though they contain a fair proportion of digestible proteids and carbohydrates.

Celery (*Apium graveolens*, L. Umbelliferae) is derived from the wild species widely spread from Sweden through Europe and the Near East. It was known to the Greeks. In cultivation it is blanched by earthing up, so as to diminish its bitterness. The feeding value is about equivalent to Winter Kale.

Spinach (*Spinacia oleracea*, L. Chenopodiaceae) was not known to the ancients. It was new to Europe in the sixteenth century, being introduced from the Near East. It is not known in the wild state. The feeding value of its leaves is below that of Kale.

The Garden Lettuce (*Lactuca scariola*: var. *sativa*, Compositae) is derived from the wild species native in temperate and southern Europe. It was used by the Greeks and Romans as a salad, and several varieties were already known to them. It is notable for its high water-content.

TABLE OF ANALYSES OF LEGUMES.

The Legumes are notable for the high proteid-content of their seeds. The water-content of the parched seeds averages about 13 per cent. Consequently the percentage of the other constituents appears to stand high as compared with the previous table, and with the analyses of Green Peas and French Beans.

Name.	Water.	Nitrogenous substances.	Fats.	Digestible carbohydrates.	Cellulose and lignin.	Ash.
Bean	13·49	25·31	1·68	48·33	8·06	3·13
Parched Peas	13·92	23·15	1·89	52·68	5·68	2·68
Lentils	12·33	25·94	1·93	52·84	3·92	3·04
Soja Beans	12·71	38·18	14·03	31·97	4·40	4·71
Arachis	7·71	31·12	46·56	9·39	2·16	3·06
Green Peas	78·44	6·35	0·53	12.00	1·87	0·81
French Beans	88·75	2·72	0·14	6·60	1·18	0·61

The Broad Bean (*Vicia Faba*, L.) was cultivated in Europe in prehistoric times. It was probably introduced during the earliest Aryan migrations, its wild habitat having been south of the Caspian, while a related species (*V. narbonensis*) is still wild in the Mediterranean region. The large percentage of proteid in the Bean is represented by numerous small aleurone grains, and the protoplasmic matrix in the cotyledonary cells, while large starch-grains account for most of the digestible carbohydrates. The thick cell-walls make up 8 per cent., while the ash is unusually high. Beans are difficult of digestion, but very nutritious.

The Garden Pea (*Pisum sativum*, L.) was introduced into Europe by the Aryans from the Near East, but it no longer exists in a wild state. It has been found among the relics of the Bronze Age, and even of the Stone Age. In point of analysis it corresponds nearly to the Bean. It is, however, commonly used in the immature state, as " green peas " ; but the analysis of these, putting aside the high water-content, corresponds in essential feeding-value to that of dried peas, while they are more readily digestible.

The Lentil (*Ervum lens*, L.) was cultivated from prehistoric times in western Asia, and in Egypt, and it has been found in the remains of the Swiss lake-dwellings, but it is no longer known in the wild state. Its analysis corresponds to that of Beans, but notably with a smaller proportion of cellulose and lignin.

The most important of all the Legumes for the future may be the Soja Bean (*Dolichos soja*, L., and other species), which is of very early cultivation in the Far East. The analysis shows that while the proteid content is extremely high, oil replaces a considerable proportion of the digestible carbohydrate. The chief supply is at present from Manchuria, but it is desirable that its cultivation should spread to Europe, and even to Britain ; as, with the exception of Rape and Linseed, no oleaginous seeds are grown in this country.

The Pea-nut, or Monkey-nut (*Arachis hypogaea*, L.) is believed to have originated in Brazil. Seeds have been found in Peruvian tombs. Thence it was conveyed to Africa and Asia, and it is now cultivated in all hot countries, either for the seeds or for the oil which they contain in so large a proportion, replacing most of the digestible carbohydrates.

The French Bean, or Haricot (*Phaseolus vulgaris*, Savi) was probably of American origin, its seeds having been found in Peruvian tombs. There is no evidence that it has been long cultivated in Europe or Asia. In its qualities and uses it resembles the Pea and Bean. Its immature pods, used as a vegetable, are inferior in food-value to green Peas.

FRUITS.

The chief interest in Fresh Fruits, apart from their high water-content, lies in the proportion of sugar and of free acids. Upon the former depends their value for the production of wines, in which the Grape takes precedence. The Vine (*Vitis vinifera*, L. Vitaceae) grows wild in W. Asia, S. Europe, and N. Africa. Both Semitic and Aryan nations knew the use of wine, and Egyptian records carry back the cultivation of the grape to 4000 B.C. The grape-sugar, of which it contains over 14 per cent., is the starting-point for alcoholic fermentation. But it is also important in the dried state, giving their value to raisins, and to dried currants, which are small dried grapes. The Apple (sugar 7·22 per cent.) and Pear (8·26 per cent.) give respectively Cider and Perry, while the Currant (6·38 per cent.) and the Gooseberry (7·03 per cent.) are also used in the preparation of British wines. But the relatively large proportion of free acids in these detracts from their value.

TABLE OF ANALYSES OF FRESH FRUITS.

Name.	Water.	Nitrogenous substances	Free acids.	Sugar.	Other digestible carbohydrates.	Cellulose and lignin.	Ash.
Apples - -	84·79	0·36	0·82	7·22	5·81	1·51	0·49
Pears - - -	83·03	0·36	0·20	8·26	3·54	4·30	0·31
Plums - - -	84·86	0·40	1·50	3·56	4·68	4·34	0·66
Peaches - -	80·03	0·65	0·92	4·48	7·17	6·06	0·69
Apricots - -	81·22	0·49	1·16	4·69	6·35	5·27	0·82
Cherries - -	79·82	0·67	0·91	10·24	1·76	6·07	0·73
Grapes - -	78·17	0·59	0·79	14·36	1·96	3·60	0·53
Strawberries -	87·66	0·54	0·93	6·28	1·46	2·32	0·81
Raspberries - -	85·74	0·40	1·42	3·86	0·66	7·44	0·48
Blackberries -	86·41	0·51	1·19	4·44	1·76	5·21	0·48
Gooseberries -	85·74	0·47	1·42	7·03	1·40	3·52	0·42
Currants - -	84·77	0·51	2·15	6·38	0·90	4·57	0·72

The actual nutritive value of fresh fruits is usually small But in the dried state those which contain sugar, and the kernels of oily nuts, are of high value, as shown by the following table:

ANALYSES OF DRIED FRUITS.

Name.	Water.	Nitrogenous substances.	Fats.	Digestible carbohydrates.	Cellulose and lignin.	Ash.
Almond - -	6·02	23·49	53·02	7·84	6·51	3·12
Hazel Nut - -	7·11	17·41	62·60	7·22	3·17	2·49
Walnut - - -	7·18	15·77	57·43	13·03	4·59	2·00
Raisins - - -	32·02	2·42	0·59	62·04	1·72	1·21
Dried Figs - -	31·20	4·01	—	49·79	—	2·86

A comparison of the constituents of kernels such as the Almond, and of dried fruits such as the Raisin or Fig, shows that together they supply in suitable proportions the proteids, fats, and digestible carbohydrates required for food.

CEREAL GRAINS.

By far the most important vegetable foods are the Cereal Grains, which are the fruits of various Grasses (Gramineae). The general construction of all of these grains is the same, and the structure of the grain of Wheat will serve to illustrate it for them all.

The Wheat-Grain is oval, and hairy at the apical end, but smooth at the base where is the scar of attachment. A lateral groove running longitudinally marks the posterior side; the anterior side is convex, and shows near its base an area which is depressed and wrinkled when dry. This marks the position of the *germ*, which is thus basal and faces the anterior side of the grain (Fig. 446). The greater part of the grain is made up of a mass of *endosperm*: this together with the germ is covered by the fruit-coat (pericarp) and seed-coat (testa), which jointly form a hard brittle shell, separated in milling from the inner parts as *Bran*.

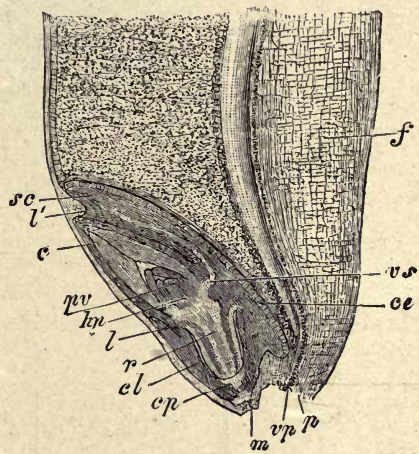


FIG. 446.

Part of a median longitudinal section of a grain of Wheat, showing embryo and scutellum (*sc*). *vs* = vasc. bundle of scutellum; *ce* = its columnar epithelium; *l′* = ligule; *c* = sheathing part of cotyledon; *pv* = vegetative cone of stem; *hp* = hypocotyl; *l* = epiblast; *r* = radicle; *cl* = root-sheath; *m* = micropyle; *f* = funiculus; *vp* = vascular bundle of funiculus; *f* = lateral wall of groove; *cp* = pericarp. (× 14.) (After Strasburger.)

A microscopic examination shows that the *germ* consists of thin-walled tissue densely stored with oily protoplasm, but with *no starch*. The *endosperm* is also thin-walled, but contains *much starch* closely packed (Fig. 447, *am*); but a superficial layer of its cells is distinguished by the absence of starch, while as it contains numerous aleurone grains it is recognised as the *aleurone-layer* (*al*). The *Bran* consists of compressed and thickened cell-walls of *woody texture*, containing a deposit of silica. The outer band (*p*) represents the fruit-coat or pericarp: the inner (*t*) represents the seed-coat or testa.

The constitution of the Wheat-Grain as shown by analysis may vary considerably according to sample. This is shown even in so important a feature as the proportion of nitrogenous substances. "Soft Wheat" may contain only 10·80 per cent. of proteid, while "Hard Wheat" has been found to contain 13·83 per cent. In some Russian Wheats it may even rise above 17 per cent. These facts are mentioned to show that the results of analysis must be taken as a general guide rather than as a statement of constant fact.

It is important as a basis for judgment of the results of milling to know by analysis the distribution of the constituent substances in the

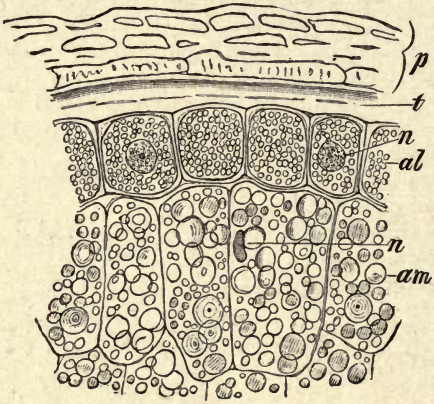


FIG. 447.
Part of a section of a grain of Wheat. *p* = pericarp; *t* = seed-coat, internal to which is the endosperm; *al* = aleurone grains; *am* = starch grains; *n* = nucleus. (× 240.) (After Strasburger.)

Wheat-Grain. This is shown by the subjoined table, taken from Dr. Hutcheson's book on *Food*:

Wheat.	Water.	Nitrogenous substances.	Fats.	Digestible carbohydrates.	Cellulose and lignin.	Ash.
Whole Grain, 100%	14·5	11·0	1·2	69·0	2·6	1·7
Bran, 13·5% - -	12·5	16·4	3·5	43·6	18·0	6·0
Endosperm, 85% -	13·0	10·5	0·8	74·3	0·7	0·7
Germ, 1·5% - -	12·5	35·7	13·1	31·2	1·8	5·7

A large portion of the grain (85 per cent.) is endosperm; the bran amounts to 13·5 per cent., and the germ only to 1·5 per cent. The latter is, however, important, for it contains a high proportion of proteids, of fats, and of ash. Since the *germ* flattens in roller-milling, it can be sifted out. The highly nitrogenous and fatty body thus extracted may then be added to ordinary flour in varying proportions, giving different kinds of germ-bread. *Bran* is characterised by its large proportion of cellulose and lignin (18 per cent.), which is indigestible by man, but more available for herbivorous animals. There is in it, however, a large quantity of nitrogenous substance, owing to the adherence of the aleurone-layer of the endosperm to the flaky scales of the fruit-coat; the silica in the latter accounts for the large percentage of ash in bran (6 per cent.). Thus bran contains an undue proportion of proteids in which the grain as a whole is deficient. Its value in bran-mash for horses is therefore easily understood. The *endosperm*, which forms 85 per cent. of the grain, is broken down in the process of milling into fine flour, semolina, and other products. Its analysis shows that, while about three-quarters of it consists of starch, there still remains in it about 10 per cent. of proteid, which, as "gluten," forms the basis of the dough of bread when moistened with water.

The purpose of milling of grain was in the first instance simply to grind it into small parts. The bread of primitive Man was doubtless "wholemeal" bread. But even in the old stone-grinding the products were usually graded roughly as bran, pollard, sharps, middlings, and fine flour. Sometimes the coarser products were reground, and the fine flour again extracted from them ; but mostly they were regarded as "offals," and were fed to stock in various forms. More recently in the process of roller-milling the grain is comminuted more accurately by successive stages, being passed through rollers with successively finer ridges. The products of these successive "breaks" are sifted partly by screens, partly by air-blasts, so arranged that their various grading can be very perfectly carried out. The end-product of greatest importance is the flour. The finer this flour is graded the less percentage of it will be yielded from the milled grain, but the whiter will be the bread. In pre-war days about 70 per cent. of the whole grain was yielded as the finest flour. Already before the war a reaction on grounds of nutrition had led to a preference for "standard flour," which was defined as "80 per cent. of the grain, with all the germ and semolina." It gave a well-flavoured, nutritious bread, but not of extreme whiteness. Since the war stricter economy has made it necessary to extract even a higher percentage of flour from the grain. The Scientific Commission of the Allied Countries has recommended a uniform milling extraction of 85 per cent. for wheat. This necessarily gives a lower grade, but no objection is possible on grounds of nutrition.

A comparison of the analyses of average samples of the grains in common use by Man gives a basis for estimating their relative values as foods. The average of a large number of different samples of each is given in the subjoined table :

TABLE OF ANALYSES OF CEREAL GRAINS.

Name.	Water.	Nitrogenous substances.	Fats.	Digestible carbohydrates.	Cellulose and lignin.	Ash.
Wheat - - -	13·37	12·04	1·91	69·07	1·90	1·71
Rye - - -	13·37	10·81	1·77	70·21	1·78	2·06
Barley - - -	14·05	9·66	1·93	66·99	4·95	2·42
Oats, average from all lands - -	12·11	10·66	4·99	58·37	10·58	3·29
Oats, England and Scotland - -	12·11	13·05	6·15	53·16	11·89	3·64
Maize - - -	13·35	10·17	4·78	68·63	1·67	1·40
Rice (not cleaned) -	11·99	6·48	1·65	70·07	6·48	3·33

Wheat (*Triticum vulgare,* Villars) has been cultivated from prehistoric times in Europe and Egypt, and in China records of it go back to 2700 B.C. It is represented by numerous varieties. Those in which the ripened grain detaches itself naturally from the husk are referred to one species (*Triticum vulgare.* Villars); those in which the ripe grain is closely contained in the husk are distinguished as Spelts (*T. Spelta.* L.). The separation of these was probably prehistoric. There is no certain evidence of the place of origin of wheat, for it is not found wild, but its probable home was in the Near East. It is the chief staple food of the white races.

Rye (*Secale cereale,* L.) probably had its origin in the countries north of the Danube, and its cultivation was hardly earlier than the Christian era. It does not greatly differ in its nutritive qualities from wheat, and is largely grown in central and northern Europe.

Barley (*Hordeum distichon,* L., *vulgare,* L., and *hexastichon,* L.) is among the most ancient of cultivated plants. It has been found wild in the Caspian region. It is chiefly used for malting and brewing, for which its low content of proteids is suitable.

The Oat (*Avena sativa,* L.) is not now found wild, but it was probably derived from a form native in Eastern Temperate Europe. It was cultivated anciently in Italy and Greece, and its grains have been found in Swiss lake-dwellings, and in early German tombs. Though a coarse grain with much cellulose and lignin in its outer coats (10 to 12 per cent.), its high percentage of fats (5 to 6 per cent.), proteids (12-13 per cent.), and ash (3 to 4 per cent.), mark it as superior to any other Cereal as a staple food. Moreover, a comparison of the average of analyses of Oats from all sources with those from England and Scotland shows that these stand the highest of all; a fact which justifies, and should encourage, the prevalent use of porridge and oat-cake.

Maize (*Zea Mays,* L.) is of American origin. At the time of the discovery of the New World it was found to be one of the staples of widespread agriculture from Peru northwards, but it has not been found in the wild state. Its large grain is very hard, by reason of the close packing of the starch-grains in the endosperm. Starch is also present in the relatively large germ. Its analysis shows a rather high percentage of fats; but the hardness of the endosperm gives a gritty texture to its products, and makes thorough cooking necessary.

Rice (*Oryza sativa,* L.) is indigenous in India, and perhaps also in China. It is a more widespread staple food than any other, supporting about one-third of the human race. It has a rough husk, which represents 6 per cent. of the grain, and is cleaned off before importation. This tends to remove the aleurone layer also, and to carry off a proportion of the proteids from a grain that is already deficient in them (6.48 per cent.). The analysis of cleaned rice, *i.e.* after removal of the husk, shows a very high percentage of digestible carbohydrates, with a marked deficiency of proteids and fats. This justifies its use in curries and puddings, in the preparation of which fats and proteids are added. But as a staple food without additions it leaves much to be desired.

INDEX AND GLOSSARY.

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